THE NEW PHYTOLOGIST

THE

NEW PHYTOLOGIST

FOUNDED BY A. G. TANSLEY IN 1902

EDITED BY

A. R. CLAPHAM, H. GODWIN, W. O. JAMES

VOLUME 44

PAGES viii AND 247

WITH NUMEROUS FIGURES IN THE TEXT

PRINTED IN GREAT BRITAIN

INDEX OF AUTHORS

INDEX OF SUBJECTS

OBSERVATIONS ON THE ANATOMICAL STRUCTURE OF THE FUCALES. I

BY F. E. FRITSCH

Department of Botany, Queen Mary College, University of London

(With 27 figures in the text)

One of the most noteworthy among the numerous features of interest presented by the Phaeophyceae is that they alone among the Algae have evolved forms with massive plant bodies displaying a parenchymatous construction and showing appreciable external and internal differentiation. The seaweeds in question are comprised in the two orders Laminariales and Fucales. Of these, the former, with their intercalary meristematic activity and their peculiar methods of thallus elaboration by progressive splitting, afford few points of parallel with higher plants. The Fucales, on the other hand, with an apical cell dominating the primary construction of the fronds, in this respect show a striking similarity with many archegoniate plants. It is therefore pertinent to inquire as to the extent of this similarity and, alternatively, to determine in what respects the Fucales present structural features peculiar to themselves. It is one of the objects of the present series of studies to provide an answer to these questions.

The usual conception of the anatomical structure of the Fucales is based very largely on that of *Fucus* and of the other Fucaceae of the intertidal zone. These seaweeds, which are characterized by early replacement of the three-sided by a four-sided apical cell and to a large extent also by dichotomous branching, are distinguished by very pronounced gelatinization, especially of the longitudinal walls, of many of the internal elements, both in the cortex and in the medulla. This change, which as shown by Oltmanns' (1922, Fig. 439) well-known figure of the apical cell of *Fucus* sets in almost immediately behind the apex, results in a resolution of much of the inner tissue of the thallus into more or less longitudinal files of cells and affords a false impression of an underlying filamentous construction. It is easy to overlook the fact that this change is a secondary one in a primarily parenchymatous structure.

A truer conception of the fundamental anatomy of the Fucales is obtained from the examination of the numerous members of the order that ordinarily grow completely submerged. These, the Cystoseiraceae and Sargassaceae (Fritsch, 1944, p. 257), many of which are inhabitants of warmer seas, possess a compact parenchymatous organization, and the younger parts of their thalli differ only in one important respect—a certain intergrading of tissues—from the kind of structure seen, for example, in the stem of an ordinary moss. Transverse and longitudinal sections of an *Halidrys* (Figs. 6, 7), *Cystoseira*, or *Sargassum* indeed show nothing of the filamentous condition recognizable in the Fucaceae, and even the disturbance resulting from hypha production is usually sensible only in the older parts.

These facts have long been known and are recorded by diverse earlier authors (Reinke, 1876, p. 357; Oltmanns, 1889, p. 49; Le Touzé, 1912, p. 42), but, since *Fucus* and its allies are always placed in the forefront of any account of the anatomy of the Fucales

(cf. e.g. Kjellman, 1897, p. 272; Oltmanns, 1922, p. 210), it is easy to obtain an incorrect idea as to what is the rule and what is the exception in this order. In actual fact the Fucaceae are the exceptional types, and their distinctive anatomical features are probably related to their usual growth between tide-levels.

Whereas the structure of *Fucus* has been examined in great detail by Reinke (1876) and Oltmanns (1889), this is not true of any member of Cystoseiraceae or Sargassaceae. It is difficult to glean from the published accounts relating to the anatomy of the members of these families how far they resemble and how far they differ from *Fucus*. Moreover, although it is known that the thallus is built up from two sources—the apical cell and the superficial meristematic layer—their respective degrees of participation are not clear. I have therefore endeavoured to work out the anatomy of a number of species of Cystoseiraceae and Sargassaceae in some detail, so far as the available material has allowed.

1. *HALIDRYS SILIQUOSA* LYNGB.

The material examined consisted of entire fertile plants of relatively small stature (up to 30 cm. long) and had been collected from Devonshire and from the Isle of Man. The two sets of specimens agreed in all essential respects and probably afford a fair picture of the anatomical features of a British *Halidrys*. The structure of the receptacles and air bladders (cf. Wille, 1889; Oltmanns, 1922, p. 212) has not been studied, attention being confined to the vegetative axes and their laterals.

Apical growth and subapical differentiation

The three-sided apical cell of this seaweed has been described and figured by Reinke (1876, p. 356) and Oltmanns (1889, p. 46). In longitudinal section (Fig. 1) it appears as a large biconvex cell with a conspicuous nucleus; the two edges run to a point at the inner end of the apical cell, while the outer end is bluntly rounded and rather broader. In transverse section (Fig. 2) the triangular shape is manifest, the sides being slightly convex. The segments, cut off from the three faces, at an early stage undergo a number of anticlinal divisions so that the segment gives rise to a curved row of four or more cells: sometimes part of the segment may divide periclinally (as in the left-hand segment in Fig. 1).

The uppermost daughter cell of each segment lengthens rapidly to produce the series of horizontally stretched cells (Fig. 1, *r*), lining the contiguous sides of the deep and narrow furrow at the base of which the apical cell lies. The lower daughter cells of each segment, broadening somewhat and dividing both periclinally and anticlinally, gradually assume a horizontal orientation. The longitudinal files of flat elements, thus produced from the lower daughter cells of the successive segments of the apical cell, form a conspicuous horizontal plate a short distance beneath the latter. They resemble in appearance a meristematic zone, although there is probably little further division at this level of the cells composing the plate. Indications of this characteristic feature are recognizable in Oltmanns's figure (1922, fig. 450) of the apical cell of *Halidrys*. Behind the apex the individual units of each file gradually lengthen, becoming first quadrangular and then increasingly rectangular as seen in longitudinal section, and so there is initiated an axial core of elongating cells (Fig. 1, *i*), which is continued backwards as the inner zone of the medulla. As the constituent cells lengthen, the end walls either remain horizontal or assume an oblique position (cf. Fig. 5, *o*) and, when the latter is the case,

adjacent elements may become dovetailed between one another. The longitudinal walls soon undergo a slight degree of thickening, but for a time at least the transverse ones remain thin.
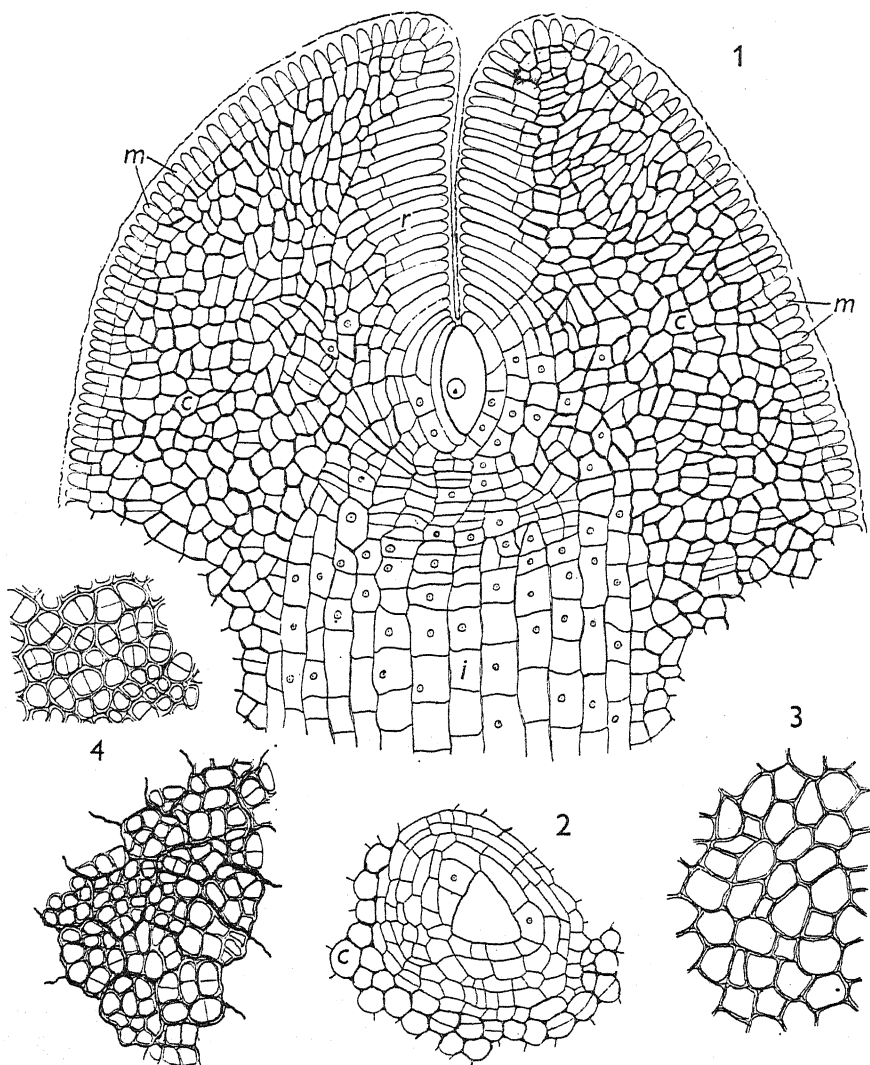
Figs. 1–4. *Halidrys siliquosa* Lyngb. 1, longitudinal section through apical cell, showing the subapical differentiation. 2, transverse section through apical cell and the elements immediately surrounding it. 3, surface view of a small part of the meristoderm from the basal part of a main axis. 4, surface views of meristoderm from growing internodes, showing above active anticlinal division of the cells, below the outlines of the underlying cortical cells. *c*, cortex; *i*, inner medulla; *m*, meristoderm; *r*, elongate cells lining furrow. (1 and 2, ×360; 3 and 4, ×570.)

The middle cells, produced by anticlinal division of the primary segments of the apical cell, undergo some enlargement and some further division, but remain approximately isodiametric (cf. Figs. 1, 2). Their walls thicken early (Fig. 2), but, even after that, there is evidently a certain amount of further division of these cells, as shown by the frequent thin septa traversing them. These cells help to build up the cortical

tissue (c) occupying the mound-like elevation surrounding the apical pit. At the same time, however, there is also some contribution from two other sources. The inner daughter cells of the segments, that go to form the basis of the medulla, may also cut off a limited number of cortical cells, while a more appreciable contribution is made from the horizontally elongated cells (Fig. 1, r) lining the furrow. These cells divide both periclinally and anticlinally and, especially towards the top of the apical pit, the inner segments cut off from them rapidly enlarge to form cortical elements. As a result, the cells composing the superficial layer become shorter and, by the time the free surface is reached, they appear as the relatively short palisade-like superficial cells (m) familiar in Fucales. The thick mucilaginous 'cuticle' extends uniformly over the whole of the surface layer.

At a level a little below that of the apical cell one can therefore distinguish, in transverse and longitudinal sections (Fig. 1) alike, three different tissues, in the main directly formed from the products of division of the original segments of the apical cell. At the surface we have the bounding layer (m) just described. Its cells are actively meristematic, undergoing repeated anticlinal and occasional periclinal divisions. The designation meristoderm, proposed by Sauvageau (1918, p. 99) for the similarly functioning layer of Laminariales, is most appropriate and will be used in the following. Beneath it there follows a broad zone of cortical cells (c) with slightly thickened walls, but still for the most part iso-diametric. In the centre is the wide axial strand (i), built up from the inner parts of the segments of the apical cell and, at this level, already contrasting with the cortical elements by elongation of the constituent cells which in general have thinner walls and in part also are slightly wider.

These three contrasting tissues derived from the segments of the apical cell present, both in their relative arrangement and in their distinctive features, a certain measure of parallel with the regions distinguishable behind the tip of archegoniate plants with a single apical cell. It can hardly be doubted that in the subapical region the elements of the axial core, whatever be their function in the older parts, serve to convey nutriment to the apical cell and to the rapidly dividing products of its activity.

The structure of the mature thallus

Already at this level, however, and even more markedly so at a few millimetres beneath the apical cell, certain changes are occurring which point the contrast with the higher plant and which are symptomatic of the peculiar organization of the Fucales as a whole. These changes are a result, on the one hand, of the activities of the *meristoderm* which bring about surface growth and add to the extent of the cortex, and, on the other hand, of progressive additions of new elements at the periphery of the medulla by conversion of the adjacent cortical cells.

Throughout most of the younger portions of the fronds anticlinal division of the meristoderm cells is in general considerably more frequent than periclinal division. In surface sections (Fig. 4) this layer appears as a system of small, closely fitted, approximately isodiametric cells. The lateral walls are straight and appear white and, even near the apex, are somewhat thickened; there is often greater thickening at the corners and the lumina tend to be rounded. The average width of the cells is 9–12 μ, but in all parts that are still growing a larger or smaller number occupy about twice the area of the others (Fig. 4), and many of these are traversed by thin anticlinal division walls (cf.

especially the upper figure). These are usually orientated in all directions so that the cells form a polygonal network without any definite arrangement, although occasional groups are recognizable which are probably derivatives of a single parent cell. Just behind the apex of a growing frond, however, the cells are in part often arranged in distinct longitudinal rows, implying a prevalence of horizontal division and of longitudinal growth. This arrangement generally disappears already at about a centimetre behind the tip, where surface growth appears to be equally distributed in all directions. On axes and laterals, which have reached their full length, the cells of the meristoderm in surface sections appear uniformly small with strongly thickened lateral walls, and few, if any, bisecting septa are recognizable. The cells of the meristoderm and the undifferentiated cells immediately underlying them always possess dense contents harbouring a considerable number of small chromatophores.

Although the importance of periclinal as compared with anticlinal division of the meristoderm cells always increases markedly in the basal parts (p. 12), local differences in this respect also occur in the younger regions. Thus, the sections through the lower part of a long lateral shown in Figs. 6 and 7 indicate fairly active periclinal division, although even here there is considerable anticlinal division. It seems that, in most of the fronds, a preponderance of periclinal over anticlinal division obtains at the nodes (i.e. the points at which laterals of one or other type arise), where the greater part of the cortex always shows a clear radial arrangement of its cells. In the internodes (Fig. 6), on the other hand, this is true only of the outermost portions. This shows that surface enlargement must diminish appreciably sooner at the nodes than in the internodes.

In surface sections cut through regions where periclinal division is not active (Fig. 4), the underlying cortical cells become visible at a lower focus and are seen to be far larger than the cells of the meristoderm, groups of eight or more of the latter corresponding to each one of the cortical cells. Since the latter are products of the periclinal division of the meristoderm cells, such pictures afford clear evidence of the greater importance of anticlinal division in the areas in question. In such sections the whitish walls of the cortical cells appear slightly undulate which is probably an artefact. In surface sections through the nodes, where the subjacent cortical cells are often of about the same diameter as the meristoderm cells, no such appearance as that shown in Fig. 4 is usually obtained.

The extensive surface growth, which is engendered by the enlargement and copious anticlinal division of the meristoderm cells in the younger parts, leads to a passive stretching of the cortical and axial elements. This operates mainly in the longitudinal direction in the latter and in the inner elements of the cortex, while the outer cortical cells may for a time be drawn out almost equally in all directions. The effects of this passive stretching on the inner elements are apparent already at a short distance below the level of the apical cell. Those composing the axial strand become markedly elongated, while the innermost cortical cells become increasingly longer (Fig. 5, *o*; cf. also the left-hand lower end of Fig. 1 and Figs. 17, 18). These elongate elements, contributed from the innermost part of the cortex, in fact rapidly approximate in length to those of the axial strand, and thus there is progressively added to the latter a somewhat similar zone which in the following is spoken of as the outer medulla. This new tissue increases gradually in width as the distance from the apex increases (cf. Figs. 9–11, *o*). Sections, cut a few millimetres behind the tip of an axis or of a long lateral, usually show only

two or three layers of cells that can be ascribed to the outer medulla, while in the older parts it is always many layers in thickness.
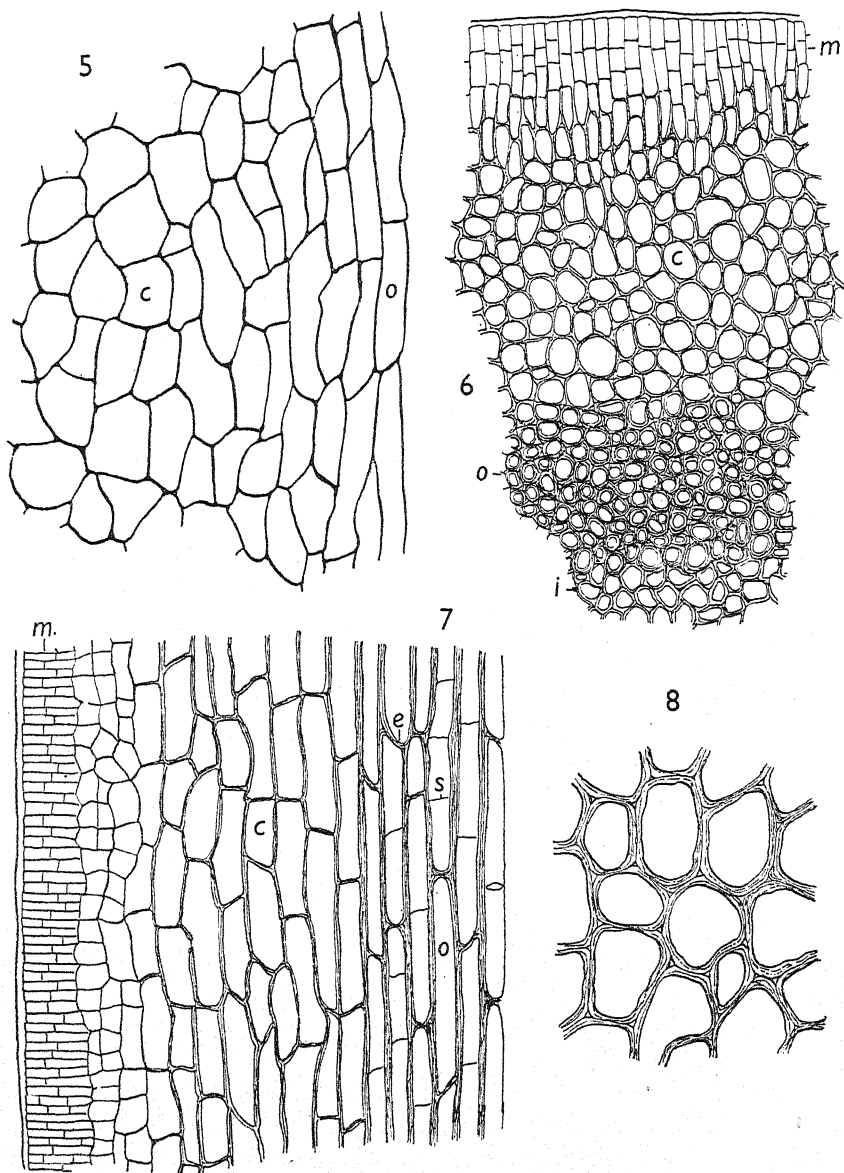
Figs. 5–8. *Halidrys siliquosa* Lyngb. 5, longitudinal section of cortical region, about 3 mm. behind the growing tip of an axis, showing early stage in formation of outer medulla. 6, part of a transverse section through one of the lower internodes of a lateral. 7, ditto, longitudinal section. 8, a few of the cortical cells from 6 on a larger scale. *c*, cortex; *e*, thickened end-walls of medullary cells; *i*, inner and *o*, outer medulla; *m*, meristoderm; *s*, septa in medullary cells. (5, × 380; 6 and 7, × 190; 8, × 500.)

As a general rule the inner and outer zones of the *medulla* are rather clearly differentiated in transverse sections (Figs. 6, 13, *i* and *o*). The cells of the outer zone, except in the youngest parts, have thicker, more distinctly lamellate walls than those composing the

inner zone; as a result, on cursory inspection under low power, the former appear rather smaller, although there is usually little difference in the actual width of the two kinds of cells. Commonly too, and especially in the younger parts, the majority of the cells of the inner medulla have sensibly denser contents than those of the outer zone. The difference in the thickening of the walls often becomes more marked in the older parts (Fig. 13), and it is in general only in the basal parts of the main axis (cf. Figs. 14, 16, *i*) and of some of the longer laterals that the cells of the inner zone undergo some further thickening; even here, however, those of the outer zone (*o*) have more markedly thickened walls. A much sharper differentiation of the two zones is obtained when production of hyphae (cf. p. 14) commences, since these elements at first appear only in the outer medulla (Figs. 10, 14) and, even in the basal parts of the axis, are far more numerous there than in the inner medulla or cortex (Figs. 11, 15, 16).

It would be plausible to speak of the inner and outer zones as primary and secondary medulla respectively, since the former is in large part at least derived from the segments of the apical cell. It is possible, however, that some of the outer elements of the inner zone have also been contributed from the cortex; in the younger parts the exact limits between the two zones are in fact by no means always clearly marked. In many sections, both transverse and longitudinal, a certain radial seriation of the cells of the outer medulla is locally recognizable and, when this is so, the cells may appear somewhat flattened in the radial direction in transverse sections; this is often more obvious opposite the edges than opposite the flat sides of the fronds. This is, however, purely a result of the radial arrangement of the inner cortical cells from which they are recruited, and there is no evidence of the occurrence of an internal meristem.

It is usually stated (Wille, 1897, p. 13; Küster, 1899, p. 828; Jönsson, 1901) that in the parenchymatous Phaeophyceae the inner elements have lost the capacity for growth and that their progressive elongation is a result of passive stretching conditioned by the active surface growth. There is no doubt in the living plant of *Halidrys* a considerable tension between the outer and inner tissues; evidence of contraction of the inner elements in preserved material is afforded by the frequent, more or less marked, undulation of their walls (cf. Fig. 18). Moreover, the ends of the medullary elements, as seen in longitudinal section, are commonly markedly rounded (Figs. 7, 21, *e*), a condition likely to be reached by the flat or pointed ends of the primary elements when the elastic walls are subjected to the marked longitudinal tension which must obtain in the region of the medulla.

At the same time there are certain facts that suggest that there may also be some active elongation on the part of the medullary elements. The transition between cortex and outer medulla, as seen in transverse sections, is often quite a gradual one. In longitudinal sections (cf. Figs. 7, 17, 18) broader cortical cells (*c*) are followed by narrower and somewhat more elongate ones, and these again by the still narrower, very elongate, elements of the outer medulla (*o*). The change, as between the last two conditions, which of course is not manifest in transverse sections, is, however, usually rather abrupt and does not appear to be altogether explicable by the assumption of mere passive stretching. Further, there is often considerable dovetailing of the medullary elements (Figs. 7, 21), suggestive of gliding growth on the part of some of them at least.

Other indirect evidence is furnished by the increase in width of the inner zone of the medulla as one passes down an axis. Figs. 9, 10 and 11 are diagrams on the same scale

of transverse sections at different levels through an axis about 18 cm. long; 9 was cut at
about 2 cm. behind the apex, 11 at about 2 cm. above the holdfast, and 10 from about
the middle. Detailed drawings of parts of similar sections are shown in Figs. 13–16.
There is no appreciable difference in the size of the elements of the inner medulla (*i*)
in the three sections, yet this tissue occupies a sensibly larger area in Fig. 11 than it
does in Fig. 10. In the uppermost section (Fig. 9) the limits of inner and outer medulla
could not be very exactly determined, on the scale of magnification used for making
these diagrams, so that the extent of increase in area as between top and middle
(Figs. 9, 10) is not clearly evident. This increase in the width of the inner zone of the
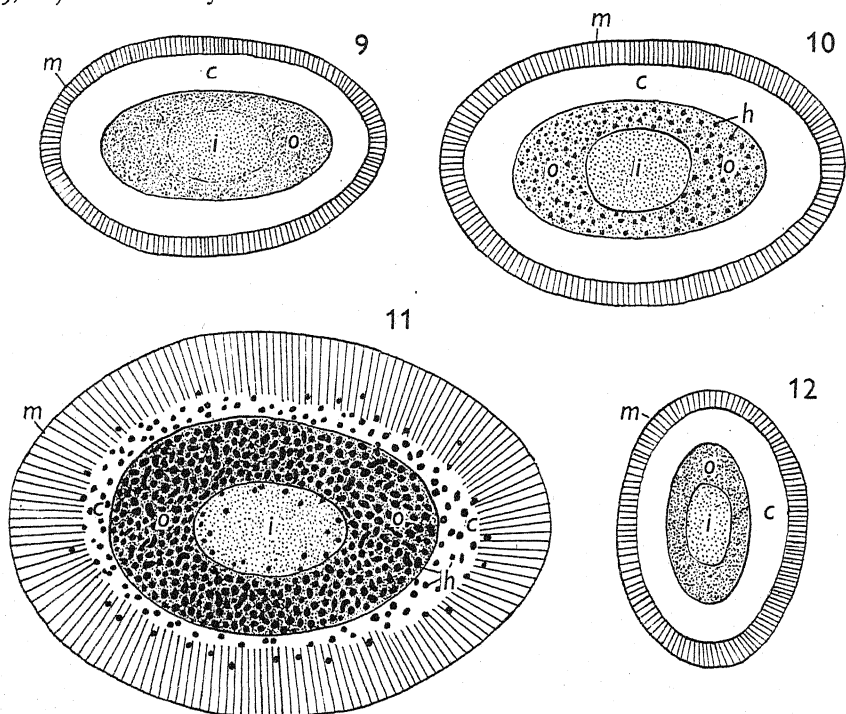
Figs. 9–12. *Halidrys siliquosa* Lyngb. 9–11, diagrams of transverse sections showing distribution of
tissues at successive levels of an axis, 18 cm. long; 9, 2 cm. behind tip; 10, middle; 11, 2 cm. above base.
Hyphae shown black. In Fig. 11 the prevalent radial arrangement of the cortex is indicated by inward
continuation of the lines marking the meristoderm. 12, diagram of transverse section, taken 6 cm. from
tip of an axis, 30 cm. long; part of this is drawn in Fig. 13. *c*, cortex; *h*, hyphae; *i*, inner and *o*, outer
medulla; *m*, meristoderm. (× 18.)

medulla is not an occasional phenomenon, but has been observed in every instance
examined and may be considerable (cf. Table 1). It is possible that the inner zone partly
increases at the expense of the outer one, a matter upon which it is difficult to get direct
evidence. It is, however, equally possible that the gliding growth suggested above is in
part responsible for the observed enlargement of the area of the inner zone. It is to be
noted that the principal enlargement (as between Figs. 10 and 11) takes place between
the levels at which the elements of the outer medullary zone are being increasingly
pushed apart by the production of hyphae.

Figs. 9–11 show that the width of the outer medullary zone may increase considerably
in the older as compared with the younger parts of the plant; as the table shows, this is

not always so pronounced. The increase is always due to the progressive accretion at the expense of the inner cortical cells which has already been dealt with above. The width of the outer zone is greater opposite the edges than opposite the flanks of the flattened fronds. Reinke (1876, p. 357), who does not deal with the mode of formation of the outer zone of the medulla, regards it as a mechanical tissue in view of the greater degree of thickening of the walls. It is possible that it functions as such, although in the younger parts the walls are by no means always markedly thickened.

The outer and inner zones of the medulla are not usually as easily distinguished in longitudinal as in transverse sections. All the elements are narrow and elongate, and there is clearly a great reduction in width as the inner cortical cells become drawn out to form elements of the outer medulla (cf. Figs. 7, 17). The length of the medullary elements varies (Fig. 7). There is no doubt that some of them attain an appreciable

Table 1. *Approximate transverse widths (in μ) of the tissues at different levels in three different axes of* Halidrys*

Axis A about 18 cm. long; B about 30 cm. long; C about 25 cm. long; B from Isle of Man, A and B from Devonshire; h in brackets indicates presence of hyphae.

Level	Zone of meristoderm†	Cortex	Outer medulla	Inner medulla
A, 2 cm. behind tip (Fig. 9)	100	420	200 (?)	400 (?)
A, middle (Fig. 10)	120	550	300 (h)	500
A, 2 cm. above base (Fig. 11)	120	700	600 (h)	650
B, 2 cm. behind tip	200	300	180	400
B, 9 cm. behind tip	200	400	240	550
B, 19 cm. behind tip	150	500	300 (?)	550 (?)
B, 22 cm. behind tip	100	450	300	600
B, 24 cm. behind tip	150	600	300 (h)	600
B, 28 cm. behind tip	100	600	400 (h)	700
C, top internode	100	450	250 (?)	300 (?)
C, 4th internode	100	450	250 (?)	350 (?)
C, 5th internode	150	400	280	350
C, 6th internode	150	400	350	400
C, 8th internode	150	400	350 (h)	500
C, 11th internode	100	450	350 (h)	550
C, 13th internode	120	480	400 (h)	500
C, 16th internode	150	750	350 (h)	600

* The measurements given refer to the regions opposite the flat sides of the fronds and are only very rough approximations. Except for the inner medulla, only the widths in one half of the section are given.

† I.e. meristoderm and the still undifferentiated cells internal to it.

length, but, since they rarely pursue a strictly longitudinal course, it has not been possible to obtain accurate measurements. The end-walls, which, as already mentioned, are often rounded but sometimes more pointed, are usually appreciably thickened (Figs. 7, 17, 18, 21), not uncommonly more markedly so than the longitudinal walls. As they lengthen, all the medullary elements, both of the inner and outer zones, undergo some division by thin horizontal or oblique septa (s). The numbers of these septa vary in the different elements and in different parts of the plant. Some of these septa probably undergo thickening and are later indistinguishable from the original end-walls. Circular unthickened areas occur on all the walls, constituting well-marked pits (p). These often appear to be more numerous in the outer (Fig. 18) than in the inner zone (Fig. 21) of the medulla, but they are nowhere really frequent.

There is direct continuity between the medulla of a lateral and that of the axis upon
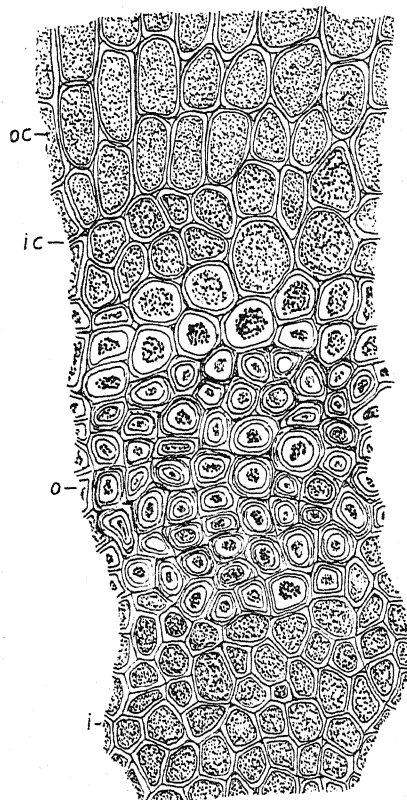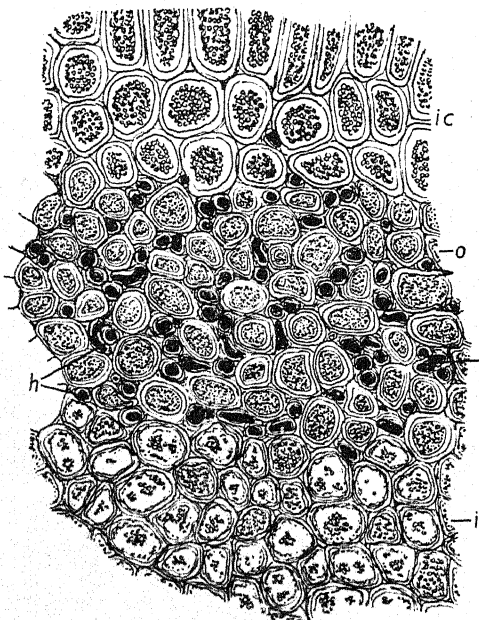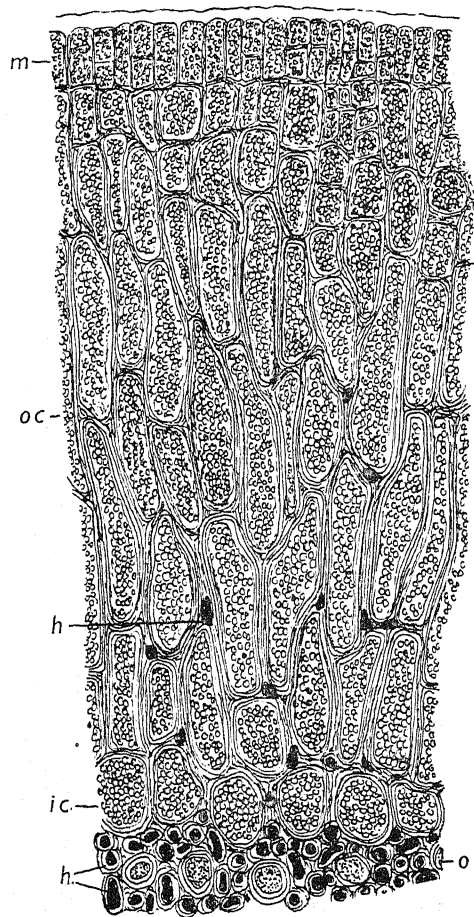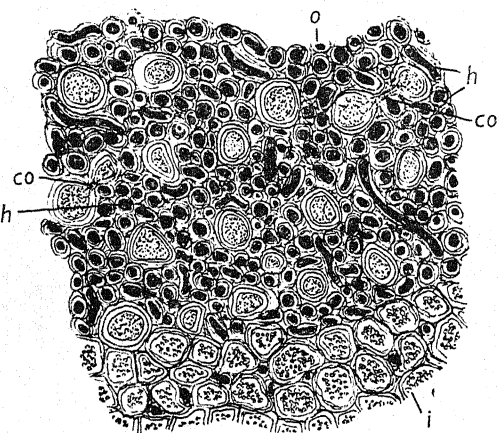
Figs. 13–16.

which it is borne. This continuity, so far as the inner medulla is concerned, is established from the earliest moment of differentiation of the lateral behind the apex. In the older parts there is also continuity between the outer zones of the medulla of a lateral and its parent axis. In the region of junction the medullary elements are in general appreciably shorter than elsewhere. In the arrested laterals, which occur as small tooth-like prominences along the edges of the fronds, there does not, however, appear to be any outer medulla and the inner zone consists of rather wide elements which may have thin or thick walls. As longitudinal sections show, the component elements are not much longer than those of the inner cortex. An elongate, but narrow, zone corresponding to the inner medulla also appears in transverse sections of the flattened receptacles, which show a parenchymatous structure throughout, like other parts of the *Halidrys* plant. In the short terete stalks bearing these structures the small medulla is circular in transverse section and a few layers of outer medulla, which fade out above, are present.

The *cortex* varies in character in different parts of the plant. Transverse sections through an internode of a growing axis or lateral show the condition depicted in Fig. 6. Only the outer cells of the cortex appear radially elongated, in conformity with their origin from the meristoderm, and a large part of the cortex (*c*) is composed of more or less rounded, isodiametric cells showing no definite arrangement. As compared with the cells recently cut off from the meristoderm, the walls appear prominently thickened and lamellose (Fig. 8). In the corners between the cells there are small spaces which seem to arise by splitting of the middle lamella, but it is improbable that they are actual cavities; they seem to be occupied by thin mucilage. In longitudinal sections (Figs. 7, 17, 23) these cells appear elongate, 2–3 times as long as broad, with square or pointed ends; it is noticeable that in such sections no clear interspaces are recognizable between them, the superposed cells fitting closely together. It is difficult to estimate how much of the cortical tissue is primary and how much is secondary, but already at a few centimetres behind the apex much of the original cortex has probably been converted into outer medulla and most, if not all, of the cortex at these levels will have been produced from the meristoderm. The appreciable tangential widening and elongation of the inner cells is an expression of the surface growth of the meristoderm discussed on p. 5.

It has already been mentioned (p. 5) that in the region of the nodes a more or less considerable part of the cortex may display a marked radial arrangement of its cells, which is probably to be ascribed to a reduction in surface enlargement of the meristoderm. Only the cells of the inner part of the cortex are rounded off in transverse section and the outer ones, though appreciably wider than the cells of the meristoderm, still tend to retain a radially elongated shape. It is probable that this condition of the nodes, and that above described for the internodes, may become permanent throughout the greater part of the length of many of the long laterals, as they mature and division of the meristoderm cells comes to an end. In many parts of such laterals (Fig. 6) the boundary

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Legends to Figs. 13–16

Figs. 13–16. *Halidrys siliquosa* Lyngb. 13, part of the transverse section of the axis shown diagrammatically in Fig. 12. 14, part of middle of transverse section shown diagrammatically in Fig. 10. 15, part of periphery and 16, part of medulla of transverse section shown diagrammatically in Fig. 11. *co*, cross-connexions between outer medullary cells; *h*, hyphae; *i*, inner and *o*, outer medulla; *ic*, inner and *oc*, outer cortex; *m*, meristoderm. (×430.)

between cortex (*c*) and outer medulla (*o*) and between the two zones of the latter (*o* and *i*) is clearly marked, suggesting that further enlargement of the tissues has ceased.

In the older basal parts of such laterals and of axes which have completed their growth, however, the cortex presents a rather different character. Here (Fig. 15) nearly the whole of it (*oc*) may consist in transverse section of radially elongated cells which are closely fitted in among one another. Only one or two layers of rounded cells (*ic*) are usually to be found at its inner limit (cf. also Fig. 14). Moreover, in longitudinal sections (Fig. 27) it is seen that, throughout the greater part of the cortex, the cells exhibit no evident lengthening in the longitudinal direction and that the majority of them are horizontally elongated and placed in very definite radial files.

This structure of the cortex in the older parts of the *Halidrys* plant is a result of great reduction in anticlinal division of the meristoderm, at a time when active periclinal division was still continuing. Longitudinal extension had probably largely ceased, although some tangential growth must still have occurred to accommodate the surface to the increasing thickness of the frond. Surface sections in these regions (Fig. 3) tend to show appreciably larger meristoderm cells (diam. $14-17\mu$) than in the younger parts and, when the underlying cortical cells can be recognised, only 2–4 meristoderm cells usually correspond to them (cf. p. 5). Moreover, it is evident that such recently formed division walls as are recognizable run prevalently in the longitudinal direction.

The walls of the cortical cells, like those of other cells, become increasingly thicker throughout the plant. In the large cortical cells of the older parts they may reach a thickness of 12μ and more. Such thick walls are always very distinctly lamellate (Fig. 26), but the lamellae appear to vary in their consistency, since some are more evident than others. In all the cells of the *Halidrys* thallus the whole of the wall is deeply stained after prolonged immersion in ruthenium red and appears to be pectic in nature throughout. No indication of the presence of cellulose was obtained with chlor-zinc-iodide. Especially in the less strongly thickened walls a middle lamella is easily recognized (Fig. 8); this is very deeply coloured by aqueous gentian violet which also stains the other parts of the wall, though less deeply. Pits (Fig. 23, *p*), similar to those found in the medullary cells, also occur in the walls of the cortical cells. They are in general rather infrequent, but are more numerous in the inner cortical cells of the older parts (cf. Fig. 18). They seem to occur on all the walls. The cortical cells are usually filled with fucosan vesicles throughout the axis, more markedly so in the older parts. These structures also usually occur copiously in the cells of the medulla. In the younger parts of the laterals they are found in much smaller numbers.

Hypha production

Large parts of the *Halidrys* plant are completely devoid of hyphae. No traces of these structures occur throughout most of the length of the majority of the laterals (cf. Fig. 6). In the axis the upper parts often show no hypha formation (Figs. 9, 13), and appreciable numbers of these structures commonly only appear at levels little more than half-way from the base (Figs. 10, 14, *h*). Sometimes, however, the formation of hyphae extends practically up to the apex of the axis, although these structures at this level are always few in number. This condition appears to occur in relatively short axes, which have probably terminated their growth in length at an early stage. In the long laterals hypha formation is usually confined to the extreme base and already at $1\frac{1}{2}$–2 cm. above their
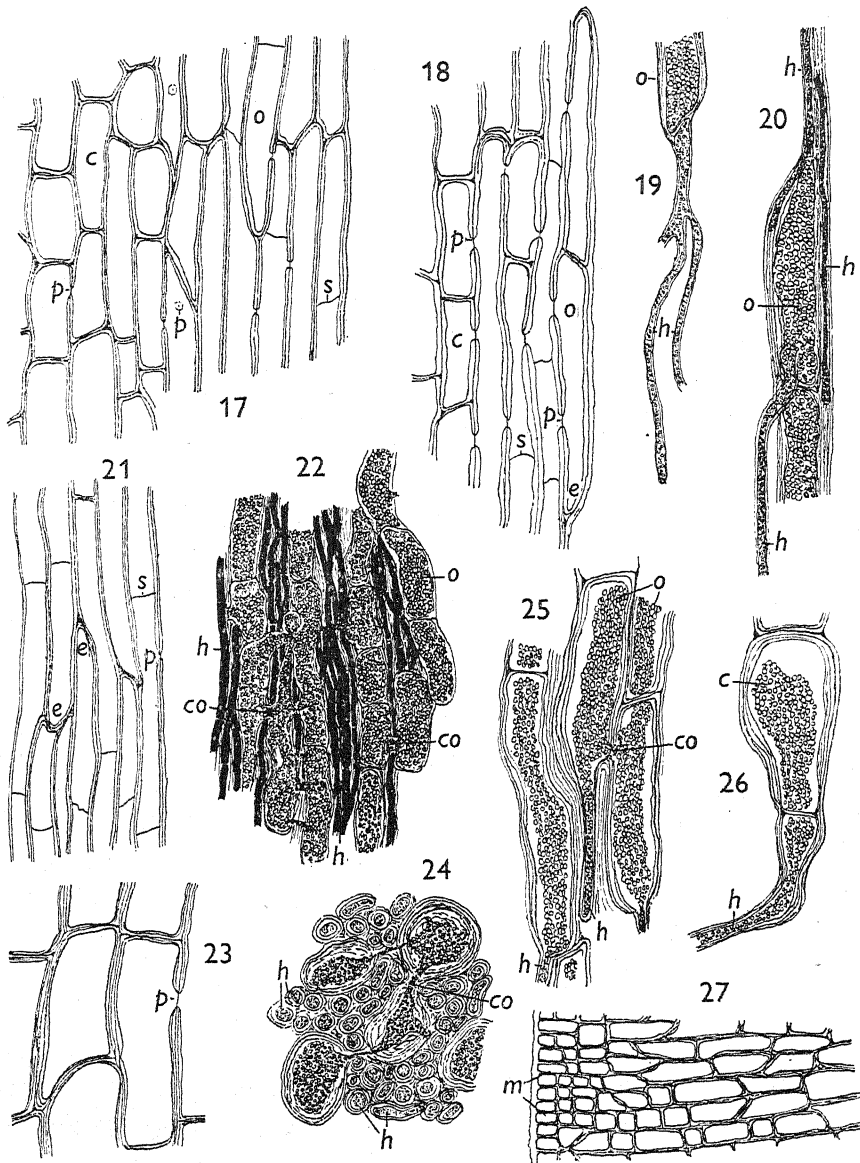
Figs. 17–27. *Halidrys siliquosa* Lyngb. 17, 18, parts of longitudinal sections through an upper internode of an axis showing transition between cortical cells and outer medulla. 19, origin of a branching hypha from lower end of outer medullary cell. 20, medullary cells with hyphae running in the walls and one arising from the side of a cell. 21, part of a longitudinal section through the inner medulla. 22, somewhat diagrammatic representation of part of a longitudinal section through the outer medulla in the basal region of the axis, showing hyphae (black) and cross-connexions. 23, cortical cells from a young internode in longitudinal section. 24, small part of a transverse section through the outer medulla in the basal part of an axis, showing hyphae and cross-connexions. 25, ditto, longitudinal section. 26, origin of a hypha from the lower end of a cortical cell. 27, longitudinal section of meristoderm and part of the cortex in the basal region of an axis. *c*, cortex; *co*, cross-connexions; *e*, thickened end-walls of medullary cells; *h*, hyphae; *m*, meristoderm; *o*, outer medullary cells; *p*, pits; *s*, septa in medullary cells. (17–21 and 23–26, × 360; 22 and 27, × 250.)

point of attachment no hyphae are generally to be found. Throughout the greater part of the length of most laterals the structure is purely parenchymatous.

Hyphae always appear at first in the outer zone of the medulla (Figs. 10, 14, *h*) and, at such levels, no signs of them are to be met with either in the cortex or in the inner medulla. They occur as small elements with dense contents and somewhat thickened walls, intercalated between the cells of the outer medulla. They run prevalently in the longitudinal direction so that in transverse sections (Fig. 14, *h*) most of them are cut through transversely. At lower levels (Figs. 11, 16) they increase very considerably in number and gradually occupy most of the area of the outer medulla, the thick-walled cells of which appear as islands amid the dense masses of hyphae. Transverse sections through such older portions show a few of the hyphae cut through longitudinally, although the vast majority still run lengthwise. At these levels (Figs. 11, 15) isolated hyphae (*h*) also appear amid the cells of the inner part of the cortex and between those of the inner medulla (Figs. 11, 16) and, in regions just above the holdfast, hyphae may be very abundant in the cortex. Even here the majority pursue a longitudinal course. Hyphae occur throughout all parts of the large holdfast which has only been quite cursorily examined.

As the cells of the outer medulla are forced apart by the intercalation of more and more hyphae between them (Fig. 16), the former remain in connection at certain points (*co*) which probably correspond to the pits found in earlier stages, although my material was not sufficiently well preserved to enable me to obtain clear evidence on this point. Certain it is, however, that, both in transverse (Fig. 24) and in longitudinal sections (Figs. 22, 25) through older parts, where abundant hyphae (*h*) have become inserted between the cells, a considerable number of such cross-connections (*co*) can be recognized. I am not in a position to say whether these are open communications or whether a membrane still separates the adjacent cell-cavities. It is probable that these connexions are ultimately ruptured by increasing intercalation of hyphae, and there is also reason to suppose that the latter process gradually leads to obliteration of some of the cells of the outer medulla.

It is by no means easy to gain accurate information as to the mode of origin and the characteristics of the hyphae. Both contents and walls present the same appearance as and stain like those of the parent cells. Since many of the hyphae pursue a somewhat tortuous course (Fig. 22), there are considerable difficulties in following up individual elements for any considerable distance. Moreover, some of them at least penetrate the walls of the surrounding cells and grow between the layers (Figs. 20, 25) and, in this condition, often appear as if they were arising from the cells in question. The most satisfactory information was provided by longitudinal sections stained with aqueous gentian violet; sections macerated by 36 hr. treatment with concentrated hydrochloric acid also afforded some useful data.

It seems that the majority of the hyphae are outgrowths from the lower ends of the medullary cells (Figs. 19, 25, *h*), but I suspect that there is also occasional development of upgrowing hyphae from the upper ends of these cells, although I have so far been unable to substantiate this fully. Hyphae also grow out in some numbers from the sides of the cells (cf. Fig. 20). There is no doubt that they often attain to a very appreciable length, although I am unable to furnish exact measurements. As already mentioned, they run for the most part longitudinally, but they rarely pursue a straight course for any considerable distance; sooner or later they tend to curve in one direction or another and to push in between other elements of the plexus. The hyphae, which appear among

the elements of the inner medulla in the older parts, are probably such deflected hyphae, since I have been unable to obtain direct evidence of their origin from the inner medullary cells.

On the other hand the hyphae that occur in increasing numbers in the inner cortex in the basal parts of the axis, are certainly in great part outgrowths of the cortical cells themselves (Fig. 26, *h*). Longitudinal sections through these regions often present a characteristic appearance; the relatively short cortical cells appear as a number of more or less lozenge-shaped areas amid the dense plexus of surrounding hyphae. In the younger parts the hyphae penetrate in the main between the cells of the outer medulla, and it is only in the older regions that they often run within the layers of the surrounding walls, (Figs. 20, 25).

Branching of the hyphae (Fig. 19, *h*) seems to occur especially near their points of origin; elsewhere as a general rule branches are found only at long intervals. Many can be followed for considerable distances without affording any evidence of branching. The huge numbers of hyphae met with in the basal parts of the axis (Fig. 16) are probably more a result of the juxtaposition of those formed at these levels and of hyphae penetrating downwards from other levels than of any copious branching on the part of these structures themselves. In the older parts the walls of the hyphae are considerably thickened and lamellose (Fig. 24, *h*), and it can hardly be doubted that the plexus formed by these structures is of marked mechanical significance. The hyphae originating in the basal regions of the laterals, penetrate into their parent axes for some distance and will serve to strengthen the connexion between the two (cf. *Ascophyllum*, Oltmanns, 1889, p. 41). In a few instances hyphae were found to be more numerous just beneath the nodes of an axis than in the regions just above and below, but this seems to be unusual. As a general rule the parts of an axis bearing well developed laterals show increasing hypha production as one passes downwards. The hyphae are septate, but their thin septa seem to occur at wide and rather variable intervals (cf. Figs. 19, 22).

<div align="center">GENERAL CONCLUSIONS</div>

While reserving a more detailed consideration for a later communication, when the facts will be discussed on a comparative basis, reference may be made here to certain general conclusions that can be drawn from this study of the anatomical structure of *Halidrys*. The basis of the three main tissues of the thallus is laid down immediately behind the apex (Fig. 1) and is supplied by the products of the segments cut off from the apical cell. In the differentiation of an axial strand of elongate cells (medulla), a superficial protective layer, and a wide intervening zone of cortex, the process is very analogous to that seen in the subapical regions of the axes of higher plants. A more direct comparison can be made with the stem of a moss.

A first great difference lies, however, in the fact that the superficial layer (meristoderm) is not only protective, but to a very high degree meristematic, and that it retains this property throughout the plant until increase in length and girth ceases. Division of the palisade-like cells of this layer takes place not only periclinally along the shortest axis, but also anticlinally along the longest axis. The former process leads to a gradual increase in thickness, the latter to an increase in surface area. In the younger parts anticlinal division usually preponderates over periclinal division and this leads to lengthening and broadening of the fronds. It is of interest that at the nodes, by comparison

to the internodes, this relation is in the opposite sense, periclinal division here usually being more active than anticlinal. A similar relation occurs also in the basal parts of the axis and of the long laterals. A detailed study of the growth of living plants of *Halidrys* in nature would be of considerable interest.

As a result of the periclinal division of the meristoderm cells the cortex is progressively replenished from the outside (Figs. 6, 7), while the surface enlargement induced by anticlinal division of these cells causes a distension of the inner cortical elements in the longitudinal direction, possibly accompanied by some active lengthening on their own part. The elongating inner cortical cells (Fig. 17) constitute a peripheral zone of increasing thickness (outer medulla) around the original medulla, a zone which differs from the latter only in the possession of thicker cell walls. By degrees the whole of the original cortex becomes converted into outer medulla and the cortex itself comes to be wholly secondary. This is very evident at the nodes and in the older parts where surface enlargement has diminished in extent so that the cortical cells retain more or less clearly the radial arrangement (Fig. 15) imposed upon them by their origin from the meristoderm.

Production of hyphae ordinarily occurs only in the older parts of the axes and in the basal region of the laterals and always commences in the outer medulla. It remains doubtful whether the inner (the original) medulla gives rise to any of these structures. At the extreme base of the axis hyphae also arise in large numbers from the secondary cortical cells. The causes operating in the formation of hyphae call for an experimental investigation. They seem to appear in regions in which surface growth in length has diminished.

There is no marked gelatinization of the cell walls in any part of the *Halidrys* thallus, although these walls become increasingly thicker in the older parts. The structure remains throughout a compact parenchymatous one, complicated however in the older parts by the intercalation of more and more numerous hyphae between the inner cells.

SUMMARY

The three main tissues (surface layer, cortex, medulla) appear immediately behind the apex of the *Halidrys* thallus and are formed from the segments of the apical cell. The meristematic activities of the surface layer in different parts of the plant are discussed in some detail, as well as its role in the replenishment of the cortex. Distension of the inner cells of the latter leads to the formation of an outer medulla of increasing thickness, which in the older parts becomes the seat of hypha formation. In the basal regions hyphae also arise from the cortical cells. The structure of the thallus is compact throughout and there is no appreciable gelatinization of the walls.

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THE SUPPOSED PRESENCE OF FORMALDEHYDE-POLYMERIZING ENZYMES IN GREEN LEAVES

By W. E. FOSTER

Department of Botany, Durham Division, University of Durham

INTRODUCTION

Present-day theories of the mechanism of photosynthesis tend to ignore the classic formaldehyde hypothesis. This is perhaps not surprising. In the first place, such theories are formulated in very general terms. In some we have analyses of the process into hypothetical types of reaction, for which evidence is sought by studying the rate of assimilation under controlled conditions. In others there are attempts to discover parts played in the process by typical physiological systems, such as those concerned with dehydrogenation or phosphorylation. One notes that these general schemata do not positively exclude formaldehyde as a possible intermediate. In the second place, some doubt has been cast on experiments that purported to show that formaldehyde could be detected by fixation in assimilating green plants, although the writer knows of no refutation of the corresponding evidence that chemosynthetic bacteria may produce formaldehyde. But the formaldehyde hypothesis is not necessarily defunct, and even if so, it may well be reborn. The following record of some relevant experiments may supply useful information to future workers. It summarizes facts and principles that the present writer will use in other connexions.

Bodnár and co-workers (1927 *a, b*) and Bodnár (1928) reported that leaves of *Tropaeolum majus*, previously killed by grinding them or drying them out at temperatures below 40° C., could convert formaldehyde, but not acetaldehyde, into reducing sugar. Preparations subjected to higher temperatures did not effect the conversion. The authors' procedure was to measure the production of reducing substance in killed green leaves, using the Ost copper-reducing method. To comparable samples either of fresh leaves ground with sand, or of dried leaf powder, were added equal volumes of water, formaldehyde, or acetaldehyde solutions. In the absence of formaldehyde, a little toluene was added as an antiseptic. After the lapse of one or more days, mercuric nitrate was added and cold aqueous extracts were made. The respective copper-reducing powers of these were measured and compared. When formaldehyde was present, the copper-reducing powers of the extracts always exceeded greatly the values yielded by comparable samples of material treated with water and toluene, or acetaldehyde solution and toluene, unless the leaf material had been previously heated to 100° C. Table 1 represents a typical set of their figures. The authors conclude that *Tropaeolum* leaves contain an enzyme system that can catalyse the condensation of formaldehyde to sugar in darkness. More recently, Paechnatz (1938) has published results that conflict with the foregoing ones. She measured the total carbohydrate content of samples of killed leaf debris to some of which formaldehyde was added. Her measurements indicated that the total carbohydrate content of comparable samples of leaf debris was unaltered whether the material were previously boiled or unboiled, or whether formaldehyde were present

in, or absent from, the preparations. Like the previously-mentioned workers, she did not estimate formaldehyde after it had been added to the leaf debris.

Table 1. *The production of reducing sugar in formaldehyde-treated leaf tissue (from Bodnár)*

Treatment of 5 g. of freshly pulped *Tropaeolum* leaves	Sugar content (in mg. of glucose) of 5 g. of the leaf tissue, after		
	0 hr.	24 hr.	48 hr.
7 c.c. of water added	31·8	33·5	35·9
7 c.c. 3 % acetaldehyde solution added	32·8	34·7	37·2
7 c.c. 3 % formaldehyde solution added	33·7	54·4	59·9
7 c.c. 3 % formaldehyde added (to previously boiled leaf tissue)	30·6	32·2	32·4

2 c.c. of toluene were added to samples without formaldehyde.

Bodnár's inference is provocative, not only because of its bearing on the formaldehyde hypothesis of photosynthesis, but because this enzyme seems to have catalysed a synthesis in leaf tissue that was autolysing, and most processes would be those of hydrolysis and general degradation. One's main criticism is that the authors did not demonstrate that formaldehyde was consumed in their preparations.* Thus Bodnár's claim rests solely on the point that leaf debris produced more reducing sugar when formaldehyde was added to it than when an equal volume of water and a little toluene were added. Clearly there are other possible explanations. For instance, formaldehyde or impurities in it might accelerate autolysis, or toluene might retard it, or both. The result in such cases would be a higher rate of production of reducing sugar when formaldehyde was present than when it was absent. Because of these considerations the work to be described in this paper was begun in 1935 and summarized then in a preliminary report. A detailed account of the work was rendered as part of a Ph.D. thesis in the University of Durham.

METHODS

A. *General*

The aim was not to make absolute estimates of the amounts of various reducing sugars and formaldehyde present in leaf extracts, but rather, by adopting a standard treatment of comparable samples of leaves, to compare the reducing figures and aldehyde concentrations obtained in the presence and absence of formaldehyde. The experimental procedure with fresh leaves was as follows: Healthy green leaf laminae of *Tropaeolum majus* were rapidly cut into strips, well mixed, and weighed out into 5 g. samples, which were rapidly ground with clean silver sand in a mortar. To each sample of pulp were added 10 or 15 c.c. quantities of water or formaldehyde solutions. To preparations that were mixed with water or very weak formaldehyde 2 c.c. of toluene were added as an antiseptic. The preparations were then incubated in corked 100 c.c. flasks at 20° C. These and subsequent operations were carried out for large numbers of duplicated samples of leaf material.

* This criticism can be levelled at all hypotheses based on the results of feeding experiments in which production alone is studied. The errors that may thus arise have been pointed out by Thomas (1940), and will be discussed in a later paper.

B. *Procedure for estimating the reducing powers of leaf extracts*

When an estimation was required, 25 c.c. of distilled water were added to each sample of the leaf debris, followed by basic lead acetate solution drop by drop, until further addition produced only a faint white turbidity in the supernatant liquid. It was found convenient to predetermine with a separate sample the volume of precipitant needed. After the mixtures had stood with the basic lead acetate for half an hour, they were filtered by suction. In each case the precipitate was washed with a few c.c. of distilled water, which were sucked through to mix with the first filtrate. The excess of lead in the filtrate was removed by adding sufficient pure sodium phosphate and filtering off the white precipitate formed. The final, faintly turbid filtrate was made up to 100 c.c. in a measuring flask. The estimation of reducing substance was performed with Benedict's solution, since this is unaffected by formaldehyde in the range of concentration encountered. Bodnár used Ost's solution, which requires corrections when formaldehyde is present. The results in Table 2 are expressed as reducing powers of 5 g. samples of leaf debris in c.c. of Benedict's solution.

C. *The estimation of the formaldehyde contents of leaf extracts*

It was found that formaldehyde could be steam-distilled and almost quantitatively recovered from pure aqueous solutions by trapping the distillates in sodium bisulphite solutions. The method of Ripper was employed to estimate it. Table 3 a indicates the order of accuracy obtainable by this means. Three solutions of pure aqueous formaldehyde were made up, of approximate strengths 1, 0·1 and 0·01 % respectively. These were accurately standardized against iodine solutions. 10 c.c. quantities of each were then steam-distilled, by the method described below, into sodium bisulphite solution. The distillates were estimated with the same iodine solutions, and thus the percentage recoveries of the aldehyde were calculated. Table 3 a shows that quantities as small as 1 mg. of formaldehyde can be steam-distilled from pure aqueous solutions with a mean recovery of 95 %, and that better percentage recoveries are obtainable with larger quantities. A procedure based on this technique was applied to leaf extracts that had contained formaldehyde. The contents of an experimental flask were strained free from coarse solids with muslin. The residue was washed, and the washings were added to the first filtrate. This extract (about 50 c.c. altogether) was then run in a thin stream from a tap funnel into the steam-distilling flask, which already contained 100 c.c. of boiling distilled water, through which a rapid blast of steam was passing. The steam-distilling process went on for $1\frac{1}{2}$ hr., and the distillate was collected in ice-cooled bisulphite solution. Table 3 b illustrates a typical set of analyses of leaf extracts obtained by this method.

RESULTS

A very large number of experiments were made using the above-mentioned methods, both on dried leaf powder and on freshly ground leaves of *Tropaeolum majus*, *Lamium album*, *Calceolaria* spp. and on leaves of grasses.

The changes of reducing power in such systems are well exemplified by the data of Table 2. These figures indicate notable increases of reducing power with time in all samples of leaf debris that were unboiled. There is no marked distinction between the increases of reducing power of samples with formaldehyde and samples without it. The

2-2

slight differences that do occur are probably no more than an expression of sampling error; there is no general tendency for formaldehyde-treated samples to develop either slightly higher or slightly lower reducing powers than water-treated ones. By contrast, boiled leaf debris never exhibits increases of reducing power comparable with those of unboiled material. One infers that the production of reducing substance in unboiled preparations is largely an enzymic process, and not merely a record of the progressive extraction, in solution, of pre-existing copper-reducing compounds in the leaf material.

Table 2. *Reducing powers of 5 g. samples of freshly ground leaf debris* of* Tropaeolum majus *to which* 10 *c.c. of water with* 2 *c.c. toluene, or* 10 *c.c. of formaldehyde solution, had been added (June* 1936)

Set	Treatment	Reducing power in c.c. of Benedict's solution				
		0 hr.	24 hr.	48 hr.	72 hr.	96 hr.
(1)	Unboiled, 2 % formaldehyde	14·9	51·7	62·3	61·9	64·7
	Unboiled, water	15·2	53·6	62·0	65·4	67·1
	Boiled, 2 % formaldehyde	23·3	—	—	—	30·3
(2)	Unboiled, 1 % formaldehyde	13·1	—	108·3	—	119·5
	Unboiled, water	13·7	—	111·7	—	120·9
	Unboiled, 0·1 % formaldehyde, 2 c.c. toluene	13·3	—	113·9	—	121·6
	Boiled, 0·1 % formaldehyde, 2 c.c. toluene	19·6	—	12·5	—	22·0
(3)	Unboiled, 0·02 % formaldehyde, 2 c.c. toluene	13·7	—	73·2	—	76·9
	Unboiled, water, 2 c.c. toluene	14·3	—	72·4	—	75·3
	Boiled, 0·02 % formaldehyde, 2 c.c. toluene	18·6	—	24·9	—	23·0

* Three separate sets of leaves were used. Set (2) contained much starch before they were ground; the others contained only a little starch.

Table 3 *b* illustrates the measured percentage recoveries of formaldehyde from the known amounts added to some of these samples. These figures may be compared with those of Table 3 *a* immediately above it. Clearly more formaldehyde is lost from solutions containing leaf debris than from pure aqueous solutions of the same strength, when one attempts to recover it from these systems by steam-distillation. For under these experimental conditions, a 100 mg. amount of formaldehyde in pure aqueous solution loses about 1 mg., a 10 mg. amount loses about 0·2 mg., and a 1 mg. amount loses 0·05 mg. as a result of steam-distillation. Expressed as percentages, these are roughly 1, 2 and 5 % respectively of the original quantity of aldehyde. When, however, leaf debris is present, a 100 mg. amount of formaldehyde now loses about 4 mg. (4 %), a 10 mg. amount loses about 1 mg. (10 %), and a 2 mg. amount loses about 0·35 mg. (18 %). Thus the percentage loss of aldehyde is greater when low concentrations are employed. The nature of this undoubted formaldehyde consumption is unknown, but Table 3 *b* shows that in comparable samples containing the same initial concentration, the consumption was about the same whether the leaf material had been previously boiled or not. Presumably there occurred a chemical combination of formaldehyde with some substances in, or produced by, the leaf debris. Other experiments have confirmed the phenomenon, and they suggest that part at least of the reaction may occur during the steam-distilling process. But we have operating here a thermostable, not a thermolabile, system.

Table 4 shows, side by side, figures for formaldehyde consumption and the corresponding production of reducing substance, calculated as hexose, by 5 g. samples of the

Table 3 *a*. *Recovery of formaldehyde from pure aqueous solutions by steam distillation*

Formaldehyde solution used	% recovery	
	Measured values	Mean
10 c.c. approximately 1 %, i.e. approximately 100 mg.	100·0, 99·1, 98·5, 99·1	99·2
10 c.c. approximately 0·1 %, i.e. approximately 10 mg.	98·7, 97·8, 97·3, 99·8	98·4
10 c.c. approximately 0·01 %, i.e. approximately 1 mg.	96·1, 93·4, 95·3, 97·6	95·6

Table 3 *b*. *Recovery of formaldehyde from* Tropaeolum *leaf debris by steam distillation* (*June* 1936)

Formaldehyde solution added	Material used	% recovery after			Mean recovery
		0 hr.	48 hr.	96 hr.	
10 c.c. 0·910 %	Boiled debris	96·6	94·7	96·5	95·9
	Unboiled debris	95·2	97·3	95·8	96·1
10 c.c. 0·100 %	Boiled debris	90·5	90·9	87·5	89·6
	Unboiled debris	92·8	94·3	89·8	92·3
10 c.c. 0·022 %	Boiled debris	85·6	78·4	81·2	81·7
	Unboiled debris	89·3	80·3	79·5	83·0

leaf debris. If formaldehyde were polymerized to reducing sugar to any marked extent, a weight of sugar would be formed equal to the weight of aldehyde consumed, and this would show in the estimations. In the unboiled preparations, a weight of hexose many times that of formaldehyde consumed is produced. Also a similar amount of reducing substance appears in unboiled preparations when no formaldehyde is added at all. In boiled leaf debris the slight and variable sugar production seems to bear no relation to formaldehyde consumption. These results support neither the theory of a thermolabile, nor that of a thermostable, polymerization of formaldehyde to reducing sugar. If any formaldehyde be transformed in such systems, it is in amounts much smaller than those recorded in Bodnár's claim (see Table 1). Very sensitive methods would be required to measure such amounts.

Table 4. *A comparison between formaldehyde consumption and reducing substance* (*calculated as hexose*) *in 5 g. samples of autolysing leaf debris* (from Tables 2 and 3 *b*)

Quantity of formaldehyde added mg.	Treatment	Formaldehyde consumed and hexose produced, after			
		48 hr.		96 hr.	
		Formaldehyde mg.	Hexose mg.	Formaldehyde mg.	Hexose mg.
		From set (2), Table 2. Much starch			
91	Unboiled	2·5	190·4	3·8	212·8
	Boiled	4·8	—	3·2	—
		From set (2), Table 2. Much starch			
10	Unboiled	0·57	201·2	1·0	216·6
	Boiled	0·91	− 14·2	1·25	+ 4·8
		From set (3), Table 2. Little starch			
2·2	Unboiled	0·43	119	0·45	126·4
	Boiled	0·48	12·6	0·41	8·8

Other possible explanations remain. Bodnár's results might be explained by supposing a stimulation, by formaldehyde, of hydrolyses taking place in his preparations. In the author's experience any production of reducing sugar in green tissue killed in the same way remains much the same whether formaldehyde is present or not. Bodnár's controls (see Table 1), in which only water and toluene were added to unboiled leaf debris, show such small increases in reducing power that the question arises whether the differences that he records may be due, not to stimulation of hydrolyses by formaldehyde, but to their suppression in the controls, perhaps by toluene. This point has been tested by using several antiseptics. Further, the question of the effect of various likely impurities in the formaldehyde used is of importance; possibly the supposedly stimulating effect of Bodnár's preparations might thus be explained.

Table 5. *Effects of various antiseptics upon the production of reducing sugar by* Tropaeolum *leaf powder*

50 g. leaf powder in	Reducing power of 25 c.c. solution after			
	20 min.	18 hr.	48 hr.	96 hr.
400 c.c. water + 0·5 % toluene by volume	18·8	103·5	117·7	125·7
400 c.c. water, 1 % toluene	18·4	102·5	118·3	124·5
400 c.c. water, excess (40 c.c.) toluene	18·6	104·1	115·8	128·0
400 c.c. water, 0·1 % phenol	18·45	103·1	115·0	123·9
400 c.c. water, 0·5 % sodium fluoride	18·7	102·0	112·7	119·1
400 c.c. water, 1 % chloroform	18·3	98·2	103·5	106·5
400 c.c. aq. solution, 0·75 % purified formaldehyde	18·4	102·7	114·7	124·0
400 c.c. aq. solution, 4 % purified formaldehyde	18·5	101·4	108·6	109·3

Table 6. *Effects of possible impurities* in formaldehyde solutions upon the production of reducing sugar by* Tropaeolum *leaf powder*

50 g. leaf powder in	Reducing power of 25 c.c. solution after		
	20 min.	16 hr.	48 hr.
400 c.c. water, 1 % toluene	18·7	103·1	118·6
400 c.c. aqueous 1 % methyl alcohol	18·4	103·6	114·3
400 c.c. aqueous 0·1 % methyl alcohol	18·9	102·6	116·6
400 c.c. aqueous 0·2 % formic acid	18·5	104·2	115·9
400 c.c. aqueous 0·01 % formic acid	18·4	105·3	115·3
400 c.c. aqueous 1 % purified formaldehyde	18·5	102·9	114·2
400 c.c. aqueous 1 % commercial formaldehyde	18·7	103·3	114·1

* The commonest impurities are formic acid and methyl alcohol.

Accordingly a series of tests upon freshly prepared leaf powder was made. Tables 5 and 6 summarize the results. These data, unlike the other analyses, were obtained by taking samples of solution from one preparation and not by using separate samples for each analysis. To 50 g. samples of leaf powder were added 400 c.c. of aqueous solutions of the various reagents. In each case the whole was thoroughly shaken to a pasty mass in a corked 1000 c.c. flask and incubated at 20° C. Samples were withdrawn by dropping some of the homogeneous paste on to a dry filter paper on a Büchner funnel, filtering rapidly, and taking 25 c.c. of the filtrate for analysis. No obvious signs of bacterial or fungal attack were observed in any of the preparations. Tables 5 and 6 show that there are no marked stimulations or depressions of reducing powers comparable with the

differences in reducing powers obtained by Bodnár (contrast Table 1). It is therefore unlikely that his figures are to be explained by a stimulation of hydrolyses by the formaldehyde or impurities in it, or by a suppression of hydrolyses in the controls.

The possibility that *p*H might influence the reactions in these systems is not mentioned by Bodnár or Paechnatz. This factor might be important in the light of our knowledge that formaldehyde is polymerized by alkalies. Indicator tests showed that the *p*H of *Tropaeolum* preparations, such as those of Table 2, was initially about 5, and fell in a few hours to a value of about 3. Experiments have been made that resembled the previously described ones, except that the suspensions of leaf debris were buffered with phosphate to *p*H's of 5·5, 7·0 and 8·2 respectively. In all of these trials the results were uniformly negative as before: no evidence was obtained that neutral or weakly alkaline leaf debris could convert formaldehyde into reducing sugar.

SUMMARY AND CONCLUSIONS

1. The claim made by Bodnár, Róth & Bernauer, that killed green tissues contain a thermolabile system capable of polymerizing formaldehyde to sugar, has been reinvestigated without confirming their results. The author has never observed any clear increase, over the controls, in the copper-reducing power of a green-leaf preparation to which formaldehyde has been added. Independent measurements, by Paechnatz, of the total carbohydrate contents of comparable samples of killed leaf tissue treated with and without formaldehyde also fail to show any differences like those obtained by Bodnár and his co-workers.

2. The treatment of samples of killed, unboiled leaf debris with pure water and a little toluene, as an antiseptic, leads to much greater increases of reducing power than those quoted, for similarly-treated samples, in the published data of Bodnár and his co-workers. Experiment shows that rapid increases of reducing power (of the order of several hundred per cent of the original number) are to be expected when leaf tissue autolyses under their experimental conditions, whether formaldehyde is present in, or absent from, the system. Negligible increases in reducing power are only obtained when the leaf material is subjected to high temperatures immediately after the cells have been injured. This is presumably due to the destruction of hydrolytic enzymes.

3. Possible explanations of Bodnár's results, based on possible differences in reducing powers due to stimulation or retardation of such hydrolyses by compounds added to the experimental system, have been examined and rejected.

4. A method for estimating formaldehyde in such systems has been described. The figures show that the measurable consumption of formaldehyde that undoubtedly occurs is controlled by a thermostable, rather than a thermolabile, system. Also there seems to be no relation between the small formaldehyde consumption and the correspondingly large production of reducing substance. If, therefore, any of the aldehyde is converted into sugar, this must be in amounts so small that they are beyond ordinary methods of estimation.

5. The foregoing evidence does not support the view of Bodnár, that green leaves contain an enzyme system capable of catalysing the conversion of formaldehyde into reducing sugar.

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ON THE ABSENCE OF A PLUMULE IN SOME LEGUMINOUS SEEDLINGS

By K. J. DORMER

Department of Botany, Queen Mary College, University of London

(With 6 figures in the text)

It has been known for some time that the seedlings of certain species of Leguminosae habitually produce, from just above the cotyledons, several shoots instead of one. Thus Lubbock (1892) found that seedlings of *Lotus tetragonolobus* always had four main shoots springing from the cotyledonary node. The phenomenon has never been thoroughly investigated, and the statements in the literature are based on superficial observations. Thus Compton (1912) says of *Scorpiurus sulcata*: 'Two or three branches arise at the cotyledonary node without reference to the cotyledons, and their internodes are very short, so that a rosette of leaves is formed.' It will be shown that this statement is quite inadequate.

Fig. 1 represents a young plant of *Scorpiurus* as seen from below. The very long and narrow cotyledons characteristic of the genus are clearly visible, as is also the cut surface of the hypocotyl. The central portion of this seedling is drawn on a larger scale, and from the upper surface, in Fig. 2. The principal shoots are four in number, two being considerably larger than the others. The larger pair are roughly at right angles to the cotyledons, while the smaller ones lie almost in the cotyledonary plane. This arrangement has been found to be constant through some dozens of specimens of *S. sulcata*, *S. vermiculata* and *S. subvillosa*. In older plants further shoots arise and to some extent obscure the regular cruciate form of the shoot-system.

In *Lotus tetragonolobus* the general appearance of the young plant is quite different, owing to the erect habit, long internodes, and compound leaves, but the arrangement of the shoots is precisely the same, with two larger and two smaller ones. The same arrangement is found again in *Securigera coronilla*.

Sections cut through seedlings at an early stage, when the first few leaves are just showing as a tuft between the cotyledons, reveal great regularity of structure. The sections illustrated (Figs. 4–6) were taken from *Lotus tetragonolobus*, but the other types examined differ only in detail. Fig. 4 represents a section through the hypocotyl and shows the vascular cylinder, slightly flattened, with the two double cotyledon traces. At a somewhat higher level, as in Fig. 5, the stele becomes contorted, undergoing constriction at certain points, and ultimately forming separate cylinders serving the various shoots. Fig. 6, which is drawn on a larger scale, shows the arrangement of the young shoots between the cotyledons; no less than seven shoots appear in this section, varying greatly in size and stage of development. They are far from being scattered at random. Associated with each cotyledon is a graded series of shoots, which we may distinguish as primary, secondary, and so on, starting with the largest. In the figure, the cotyledons have been labelled A and B, so that $A3$ is the tertiary bud of cotyledon A,

and similarly for the others. It will be observed that successive members of each series are placed alternately right and left of the midrib of the corresponding cotyledon, the higher members being further out from the central axis of the seedling. There is no vestige of any central structure, the two primary shoots being in direct contact below.
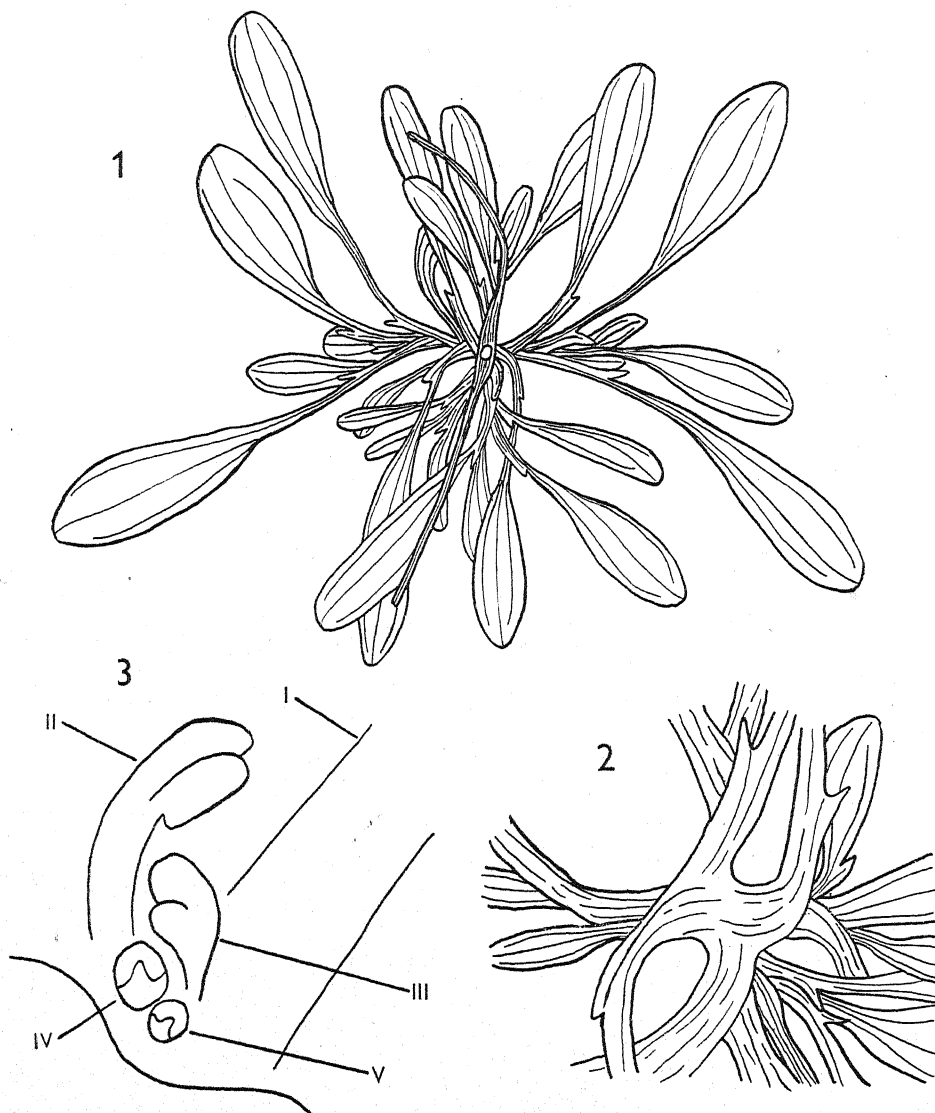
Figs. 1–3. 1. Young plant of *Scorpiurus* sp. seen from below, ½ natural size. 2. Central part of same plant, seen from above, on a larger scale. 3. Axillary buds of a leaf of *Pisum sativum*, from the abaxial side. The buds are numbered in descending order of magnitude.

Nor is there any indication that any vascular strands remain at the centre when the supply to these shoots is drawn off.

This structure is so unlike the usual arrangement, which is found in many forms closely allied to those which we are considering, that its interpretation is a matter of

some urgency. To speak simply of a polychotomy of the plumule is not sufficient, since such a hypothesis does not account for the regular way in which the shoots are arranged. Nor is there anything to indicate that any shoot is lateral to another. The key to the problem appears to lie in certain peculiarities of axillary branching in Leguminosae.
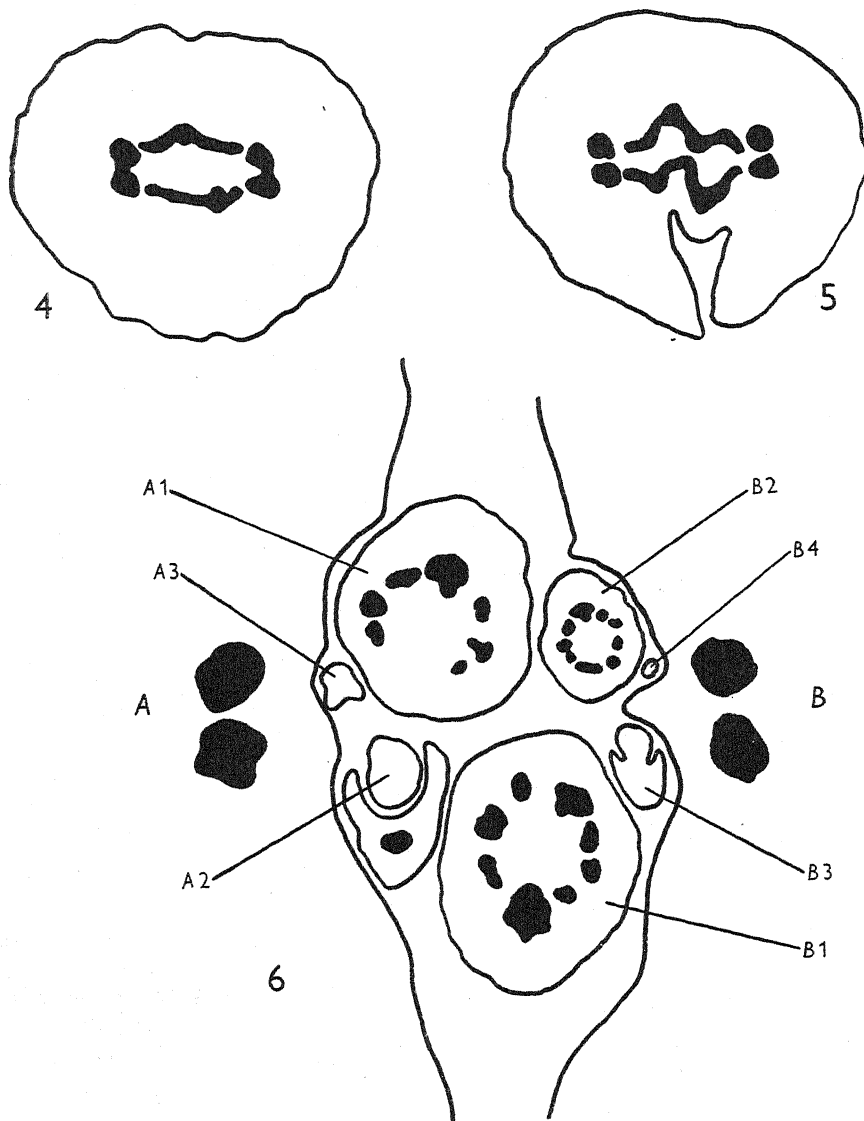
Figs. 4–6. Transverse sections of a seedling of *Lotus tetragonolobus*. 4 and 5, ×20; 6, ×45. In Fig. 6, *A* and *B* are the cotyledons, while *B*2 is the secondary bud of cotyledon *B*, and so on.

The occurrence of more than one bud in the axil of a leaf is a phenomenon which has attracted a good deal of attention, and it has been shown (Russell, 1892) that in many Leguminosae there is a whole series of buds in the leaf-axil. Fig. 3 represents the axillary buds of a leaf of *Pisum sativum*, as seen from the abaxial side. The Roman numerals

refer to descending order of magnitude, and it will be seen that the buds form a graded zigzag sequence, the primary being too large to be shown in its entirety, while the two smallest are mere papillae, each with a slight ridge representing its first leaf. The first leaf of each shoot is turned away from the central line of the bud series, as is also the case in the anomalous seedlings. There appears to be no definite limit to the number of buds in the series. Vigorous specimens produce more than feeble ones, and some species yield higher numbers than others, but potentially the series seems capable of indefinite extension. If the primary is destroyed, it is replaced by the secondary, and so on. Now it has been found in several species having normal epicotyledonary structure, that if the plumule is cut off at an early stage, each cotyledon produces a range of axillary buds, and the two primaries (and often also others) grow out to replace the lost plumule. Obviously, if the plumule were suppressed, the plant would have exactly the structure found in the anomalous types which are the subject of this paper. We may conclude that in *Scorpiurus* and similar forms, the plumular shoot has been suppressed, so that the whole epicotyledonary part of the plant is formed by the axillary buds of the cotyledons, these buds being arranged in precisely the same manner as is usual for the buds of foliage leaves in the family.

The absence of a true plumule is of particular interest in that the forms in which it is known to occur are placed, in all generally accepted classifications of the Leguminosae (e.g. Taubert, 1891), in two different tribes, the Loteae and the Hedysareae-Coronillinae. The anomaly therefore lends support to the view, which will be developed in a further publication, that these two groups are, in fact, closely related. As normal seedlings also occur in both tribes, the character may prove to be of great taxonomic importance.

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COASTAL PEAT-BEDS OF THE NORTH SEA REGION, AS INDICES OF LAND- AND SEA-LEVEL CHANGES

By H. GODWIN

The Botany School, Cambridge

(With 23 figures in the text)

CONTENTS

A. INTRODUCTION

This paper is intended to carry a stage further the examination of the general principles of the pollen-analysis method in its major applications to the territories of the Atlantic fringe of Europe. It has already been shown that a simple zonation of the pollen diagrams so far available from England and Wales can be made to yield a consistent picture of the forest history in those countries throughout post-glacial times. This zonation already has been given a fair degree of correlation within England and Wales, with archaeological horizons, and in a recent paper (Godwin, 1943) I have attempted to show that interesting and useful correlations may be made also between the stages of forest history and the different phases of change in relative land- and sea-level which are indicated in coastal deposits round these islands.

Although the correlations achieved between forest history and archaeology and the drift of land- and sea-level movements thus promise an ultimately satisfactory *internal* scheme for the British Isles, we have not hitherto been able to link such a scheme to the similar schemes worked out for the proximal parts of the European continent. Very considerable issues hang upon the establishment of some valid general scheme embracing at once the post-glacial history of the British Isles and of the Continental margin. The serious difficulty presented by lack of such a scheme turns upon the uncertainty we find in transferring the relatively assured Scandinavian time-scale across the North Sea to this country, and the dubiety of isolated attempts to co-ordinate with the continental changes, any events—climatic, geological, or archaeological, which appear in our own post-glacial history.

B. CO-ORDINATION OF POLLEN-ANALYSIS DATA

The present paper is a preliminary essay towards a simple correlation with the region of the Continental margin, and has been produced in the following way. Examination of the pollen diagrams from all parts of Britain (especially England and Wales) has shown that certain zones and the horizons separating these zones are consistently recognizable over the whole country. We have taken the most important horizons and have

sought to recognize them in a selected series of suitable pollen-analysis sites distributed along the Continental coastal lowlands from southern Sweden southwards to Holland. These sites are chosen so that their pollen profiles, whilst covering as large a part of the post-glacial period as possible, truly reflect the general forest cover of the lowland plains, being influenced little by highland and its substantial effects upon forest dominance, and equally little by local growths of alder, birch or pine upon dried-out bog- or fen-surfaces. The profiles chosen for this purpose are listed below.

Site	Country	Author
Veelerveen	Holland	Eshuis
Vriezenveen I	,,	Florschütz & Wassink
Korenburgerveen	,,	ten Houten
Alt Hattlich	,,	Schwickerath
Sager Meer	N.W. Germany	Erdtman
Erndtebrück	,,	Budde
An den drei Putten	,,	Overbeck & Schmitz
Fresenburgsmoor	,,	Schubert
Dannenburg	,,	Overbeck & Schneider
Elmer Hohenmoor	,,	Schubert
Melbeck I	,,	Overbeck & Schneider
Langenmoor	,,	Schubert
Kollund	Schleswig	Ernst
Bundsø	,,	Jessen
Hornholz	,,	,,
Brøndum	Denmark	Hanson & Jessen
Asfærg	,,	Erikson & Jessen
Svanemose	,,	Jessen
Tengslemark-Klintesø	,	,,
Kragsø	,,	Jonassen
Ageröds mosse	S. Sweden	Nilsson.

These sites are indicated in Fig. 1.

In each diagram six horizons have been sought. These, accompanied by the contractions employed to mark them in the figures, are loosely defined as follows:

P.G. The end of the late-glacial and the opening of the post-glacial, as indicated by the sudden increase in the ratio of tree to total non-tree pollen. This corresponds with the transition from zone IV to zone V in the pollen zonation for England and Wales.

H. The time when the sudden rapid extension of Hazel (*Corylus*) begins, causing low values or absence of this pollen to be quickly replaced by very high percentages. This is the beginning of zone V on the English scale.

B.A.T. What may roughly be called the Boreal-Atlantic transition. This is the horizon which, following the first extension of hazel and oak, elm and lime, is indicated by the sudden expansion of alder to dominance, with recession of pine but no diminution of the warmth-loving trees. This is the transition from zone VI to zone VII on the English scale.

G.H. This is the horizon of the *Grenzhorizont*, which has been recognized as falling at the sub-Boreal to sub-Atlantic transition. It is indicated stratigraphically in many profiles and this has been accepted in such instances as evidence for determining the horizon in the pollen series. In the numerous recurrence surfaces described by Granlund for south Sweden this corresponds to R.Y. III.

Pr. This is the present day, reached, of course, only in profiles from bogs still growing.

Ul. This is a rather subsidiary horizon between *B.A.T.* and *G.H.*, where the previously high elm (*Ulmus*) pollen values show a sharp decrease to subsequently maintained low values. Pine commonly shows a similar diminution, and less often lime (*Tilia*). On the English scale this horizon marks the transition between subzones VII*a* and VII*b*.

Fig. 1. Map of North Sea region showing sites referred to in the text.
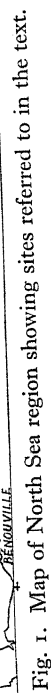
All six of these horizons are in fairly general use as the basis of pollen-analysis zonation in the region we are concerned with (Table 1). Each of the chosen pollen profiles has been redrawn with a uniform vertical scale based upon the assumption of data given above. They have been grouped into four regional diagrams so as to simplify direct comparison (Figs. 2–5).

In France there are no sufficiently long or detailed series from the lowland plain, and in Belgium the only adequate series, that from Alt Hattlich, comes from a high altitude in the Hohes Venn (Schwickerath, 1937) and is included to demonstrate the modifying influence of altitude. Alongside it and included for the same purpose, is the series from Erndtebrück in the Sauerland, which lies east of the Rhine at the edge of the great German coastal plain. A series of great raised-bogs lies along a great part of the Dutch-German frontier, and from these come the selected series at Korenburgerveen, Vriezenveen and Vielerveen. Similarly, between the Ems and the Elbe lie great stretches of raised-bog, and from the many series available here we have employed only An den

Table 1

	Approx. dates	Nilsson (S. Sweden)	Jessen (Denmark)	Godwin (England and Wales)
Pr.	A.D. 1940	I II	IX	VIII
G.H.	500 B.C.	III IV	VIII	VII–VIII VII*b*
Ul.	3500 B.C.	V VI VII	VII	VII*a*
B.A.T.	6200 B.C.	VIII	VI V	VI
H.	7500 B.C.	IX	IV	V
P.G.	8000 B.C.	X	III	IV

drei Putten, Fresenburgsmoor, Elmer Hohenmoor, Dannenburg and Melbeck I. In the third diagram have been grouped series from Kollund, Bundsø, Hornholz in Schleswig and one from Langenmoor, which lies nearly in Hanover just across the estuary of the Elbe. In Fig. 4 are the five Danish sites, Svanemosse, Kragsø, Asfærg, Brøndum, in Jutland, and Tengslemark, near Klintsø, in the north of Zealand. We have included but one series from south Sweden, that from Ageröds mosse, but the very detailed and extensive comparative studies by T. Nilsson of pollen diagrams from the bogs of south Sweden leave one in no doubt how far one can regard the Agerödsmosse profile as typical. The twenty-one profiles here matched with one another extend no farther north than the latitude of Aberdeen and, with the exception of Alt Hattlich, do not lie so far south as London.

Neglecting the two high-altitude diagrams of Alt Hattlich and Erndtebrück, the whole of this collection demonstrates a very considerable similarity in forest history, and alignment on the six given horizons indicates great consistency in behaviour. Each diagram that is old enough shows a basal birch-pine period succeeded by one in which pine has increased relatively to birch, though both remain decisively predominant over all other

trees. In this pine-dominated phase the hazel values are often very high, and here also the elm, oak, lime and alder appear in small amounts. At the line *B.A.T.*, in all diagrams the alder values show a sudden rise and thereafter maintain high values, and along with substantial amounts of oak, elm and lime, this pollen generally preponderates over pine and birch. The upper part of the diagrams is rather uneventful, but at the *G.H.* line in all of them, *Tilia* is greatly reduced, whilst above it *Fagus* increases much in importance. It is reasonable to consider such differences as exist between these diagrams to be caused by small local differences such as those of soil and aspect. These we may regard as perhaps responsible for the maintenance in Melbeck I of high pine values well above *B.A.T.*, and of the prevalence of birch throughout the whole sequence at Brøndum. The least obvious of the horizons employed is *Ul.*, but even this is quite evident in a number of the diagrams. It ought to be emphasized that the line *G.H.*, though consistent in respect of the drift of the pollen curves, was chosen in the individual diagrams largely on the basis of stratigraphic evidence for this major recurrence surface.

Let us now consider separately and briefly the four regions covered by the respective Figs. 2–5. The curves from the Netherlands (Fig. 2) are representative of the general run of the diagrams produced by Vermeer-Louman (1934), Florschütz and Wassink (1935, etc.), Polak (1936), ten Houten (1935), Eshuis (1936), and Erdtman (1928). Of the four lowland sites, Veelerveen, Sager Meer and Vriezenveen I show much similarity, but Korenburgerveen is abnormal in showing no hazel maximum and no preliminary extension of elm, oak and lime before the sudden expansion of alder. In this profile the early expansion of alder is associated with a layer of alder-wood peat, so that the true position for the *B.A.T.* horizon is in doubt, and indeed it is possible that there is a gap in the pollen sequence. The *Ul.* horizon is weakly marked in all four diagrams, and elm is in fact present only to a small extent in any of them. Much interest surrounds the behaviour of the beech curves, for they might be expected to serve as indices to a subdivision of the upper parts of the scale of forest history. Eshuis (1936) has summarized the range of behaviour of the *Fagus* curves in the Dutch diagrams, and this range is illustrated also by our Fig. 2. In some diagrams the *Fagus* curve only begins at the *G.H.* horizon (e.g. Vriezenveen I and Valthermond), in others the *Fagus* curve is present more or less continuously below the *G.H.* level but not below the *Ul.* horizon, and may form a temporary maximum between these two levels, though not so large a one as that formed later above the *G.H.* (e.g. Veelerveen and Sager Meer (Fig. 2), also Hoornderveen and Veenhuizer Stukken (Eshuis)). Finally, we may have the *Fagus* curve present continuously from not far above the *B.A.T.* horizon, but again showing much expansion above *G.H.* (e.g. Korenburgerveen in Fig. 2). I think the problem of how to regard these variations in behaviour is simplified by considering the diagram from Alt Hattlich in the Hohes Venn. Here the altitude of 620 m. above sea-level is such that the site lies within the beech forest zone of to-day, and correspondingly the period after the *G.H.* horizon has so much *Fagus* pollen that it can be regarded as a 'beech period', and substantial amounts of beech are also found throughout the whole period between *B.A.T.* and *G.H.* An even more striking instance of the modifications produced on the edge of the European coastal plain by high altitudes is shown in the short diagram for Erndtebrück in the Sauerland. At this site, 470 m. above sea-level, not only is beech preponderant above *G.H.* but also for some distance below it (Fig. 2).

It seems generally clear that in the Dutch lowland diagrams some sites have favoured
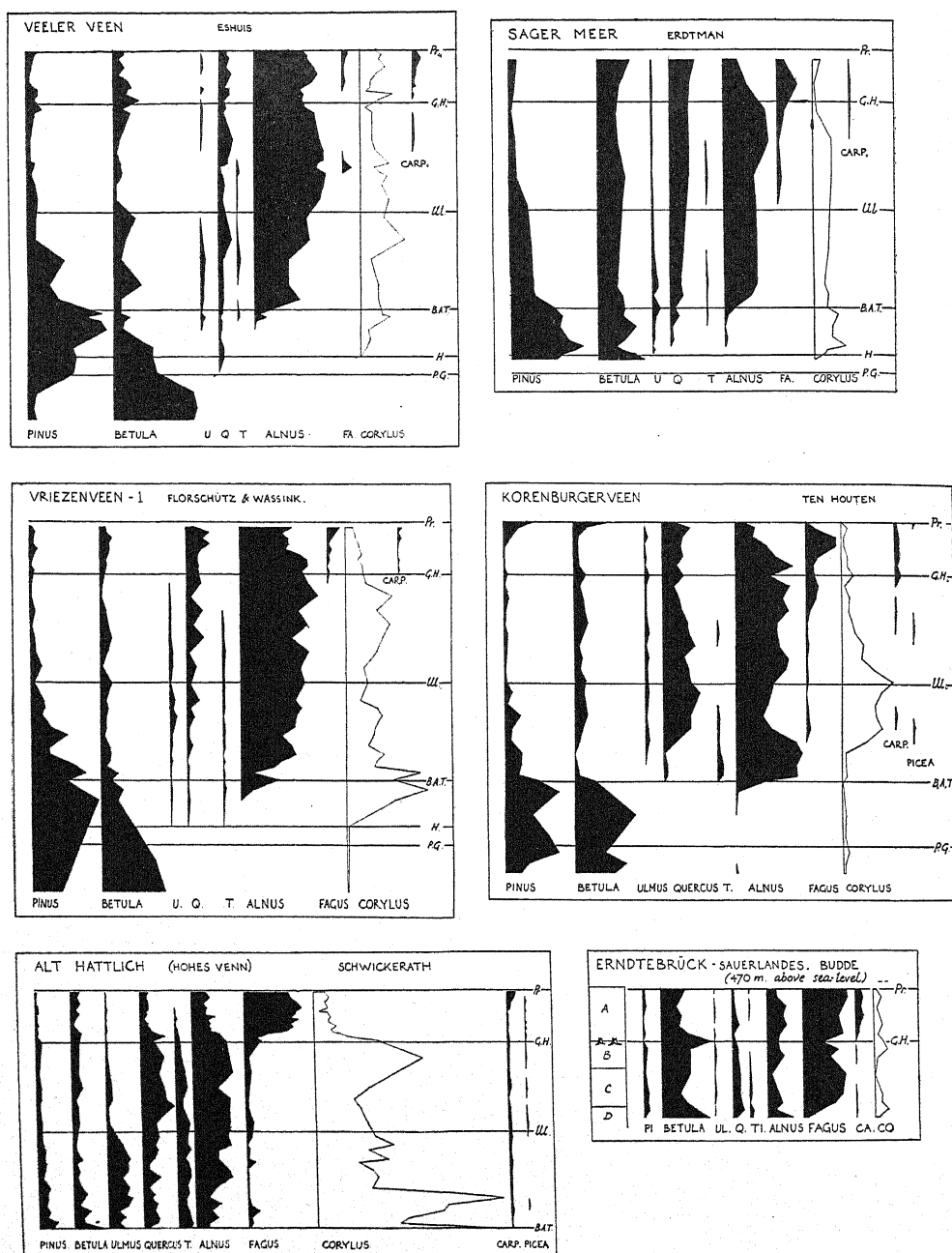
Fig. 2. Co-ordination diagram of lowland pollen series from Holland and Germany. (The two lowest are high-altitude sites included for contrast.) All have been reduced to a common vertical scale, based on recognition of the horizons shown.

beech throughout, or have been specially influenced by nearness to the mountain beech forests, and these have both high beech values above *G.H.* and also early and good representation of beech below *G.H.* The less-favoured sites have had both smaller maxima above *G.H.* and feebler representation below it. In using, therefore, the beech pollen to date some peat deposit of otherwise doubtful age, it is clear we must be guided more by the *drift* of the beech-pollen curves than by the absolute amounts they indicate at any given level.

The hornbeam pollen very closely reflects the situation for beech, but the values are consistently so much smaller that we can most usefully employ them only as confirmatory of conclusions based on the beech curves. The tendency of *Carpinus* to expand above *G.H.* is, however, quite consistently demonstrated in the Dutch curves. In relation to the dating of phases of forest history in the Netherlands it should not be overlooked that a bronze hoard referable to the second period of Montelius, 1600–1400 B.C., was discovered 'in the Grenz peat'. In fact the pollen analyses at the site indicate the hoard to lie some 25 cm. underneath the actual *Grenzhorizont* (Florschütz & Wassink, 1935).

The five north-west German sites in Fig. 3 show great resemblances, the beech and hornbeam curves all having maxima above *G.H.* and smaller values below. Melbeck I is much the most easterly of the five sites, and differs from the rest both in the low but regular amounts of spruce pollen from *B.A.T.* onwards, and in the somewhat stronger influence of pine throughout. Melbeck and Dannenburg are alike in the tendency of both elm and lime to persist in small amounts after *G.H.* Very considerable information as to the forest history of the north-west German coastal plain has been gathered, especially by Overbeck and his pupils (see p. 44), and a good collection of pollen diagrams is available for the area. Regional differences from east to west within this area are recognized by these workers, but they are not of large magnitude. Generally speaking, they involve higher values for pine, beech, and hornbeam in the east, and for lime, oak, and hazel in the west. It is Overbeck's conclusion (1934) that in general *Fagus* pollen is regularly present 'in the second half of the Atlantic period', though practically absent before this. His view is supported both by the curves of Fig. 3 and by the analyses of other workers given in Table 2 (p. 37), from which it will be seen that the *Ul.* horizon is usually characterized by very low values of beech pollen: these rise towards the *G.H.* level, and beyond to values indicated as '*Fagus* Maximum' (*F.M.*).

Schubert (1933) records a number of archaeological finds with associated pollen and stratigraphic analyses, which lend certainty to our extension of the six primary horizons over this part of Germany. Thus at Minstedt a bronze axe (Montelius II) was found some distance below *G.H.* A Neolithic stone axe found at Islersheim was some 120 cm. below *G.H.*, and certainly between that and the *B.A.T.* horizon, although impossible to place in relation to the *Ul.* level.

In Fig. 4 there are three diagrams from Schleswig-Holstein and one (Langenmoor) from just across the estuary of the Elbe. These again broadly resemble one another, and show no great departures in type from those already considered. Although the values of *Tilia* just before and just after the *B.A.T.* horizon at Bundsø are strikingly high, this feature has also been recorded in several profiles from north-west Germany. In all four of the diagrams there is a fairly pronounced break in the run of the pollen curves at the *Ul.* level.

Lastly, in Fig. 5, we come to consider five sites from Denmark with the single linking diagram from Ageröds mosse in south Sweden. The general pattern of the elegant detailed Swedish diagram is recognizable in the other five, and this northerly group as a whole
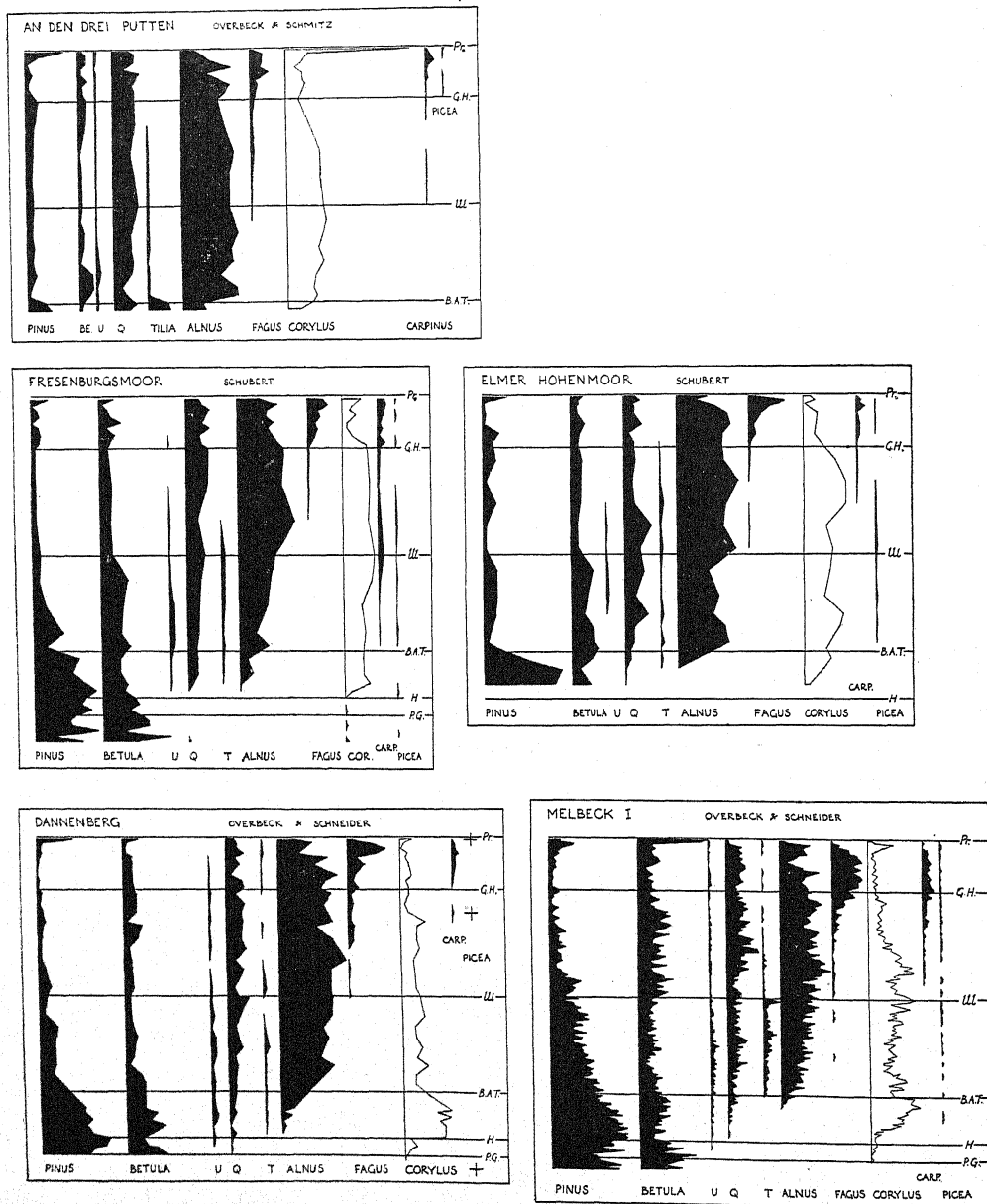
Fig. 3. Co-ordination diagram of lowland pollen series in north-west Germany, all reduced to a common vertical scale.

behaves very conformably with those already discussed, although birch tends to be rather more important and to show more pronounced revertence at the top of the diagrams. Lime and elm are also rather more important, so that they have quite substantial values

Table 2

Site	Position	% *Fagus* at					% *Carpinus* at				
		B.A.T.	Ul.	G.H.	F.M.	Pr.	B.A.T.	Ul.	G.H.	F.M.	Pr.
(D. Schroeder, 1930)											
Bergedorf (1)	18 km. N.N.E. Bremen	o	+	7	31	21	o	?+	+	7	7
,, (3)	,, ,, ,,	o	+	4	17	25	o	+	1	8	7
Seehausen	,, ,, ,,	o	1	2	17	20	o	+	+	9	7
Worpedahl	,, ,, ,,	o	1	3	17	8	o	+	2	8	2
Worpeswede	,, ,, ,,	o	1	13	38	27	o	+	4	6	5
Tarmstedtermoor	,, ,, ,,	o	+	3	12	22	o	–	+	7	8
(W. Selle, 1935)											
Grosses Moor	Lüneberger Heide	o	1	20	28	5	o	1	3	19	1
,, ,,	,, ,,	o	1	16	25	5	o	+	3	18	1
,, ,,	,, ,,	o	1	9	32	–	o	+	2	8	?
,, ,,	,, ,,	o	+	6	19	–	o	+	4	8	?
Ochsen Moor	8 km. W.S.W. Wittingen	o	+	6	17	11	o	+	1	9	5
,, ,,	,, ,,	o	2	16	23	12	o	?	2	2	2
Schweimker Moor	12 km. N.W. Wittingen	–	–	8	29	8	o	–	1	9	4
Vogelmoor	17 km. N.E. Gifhorn	o	1	6	15	–	o	1	3	2	–
,, ,,	,, ,,	–	–	2	8	–	o	–	+	4	–
Zuschneide	24 km. E.N.E. Gifhorn	o	+	11	12	–	o	+	3	2	–

o = absence, — = no data.
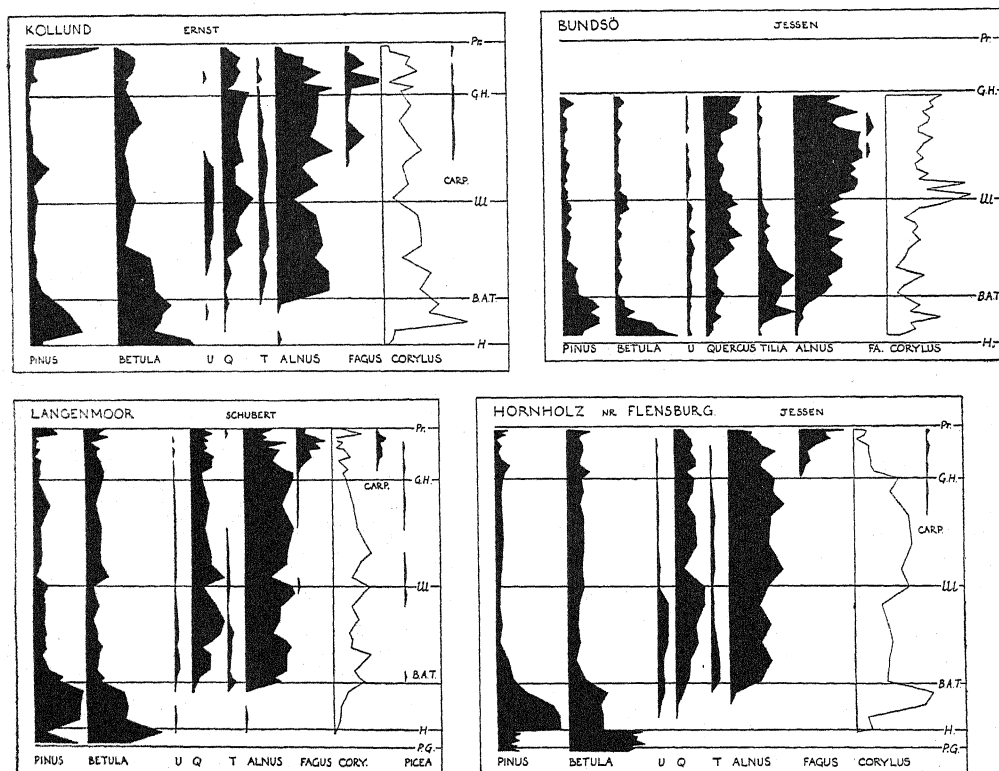
Fig. 4. Co-ordination diagram of lowland pollen series in Denmark and Schleswig-Holstein, all reduced to a common vertical scale.

before the *Ul.* level, and do not disappear altogether above *G.H.* Within the group we have the range of behaviour of the beech curves that has been remarked in the other regions: above *G.H.* it is very abundant at Svanemose, abundant at Asfærg and Ageröds mosse and rare at Brøndum: the Klinteso diagram stops short at *G.H.* We have already
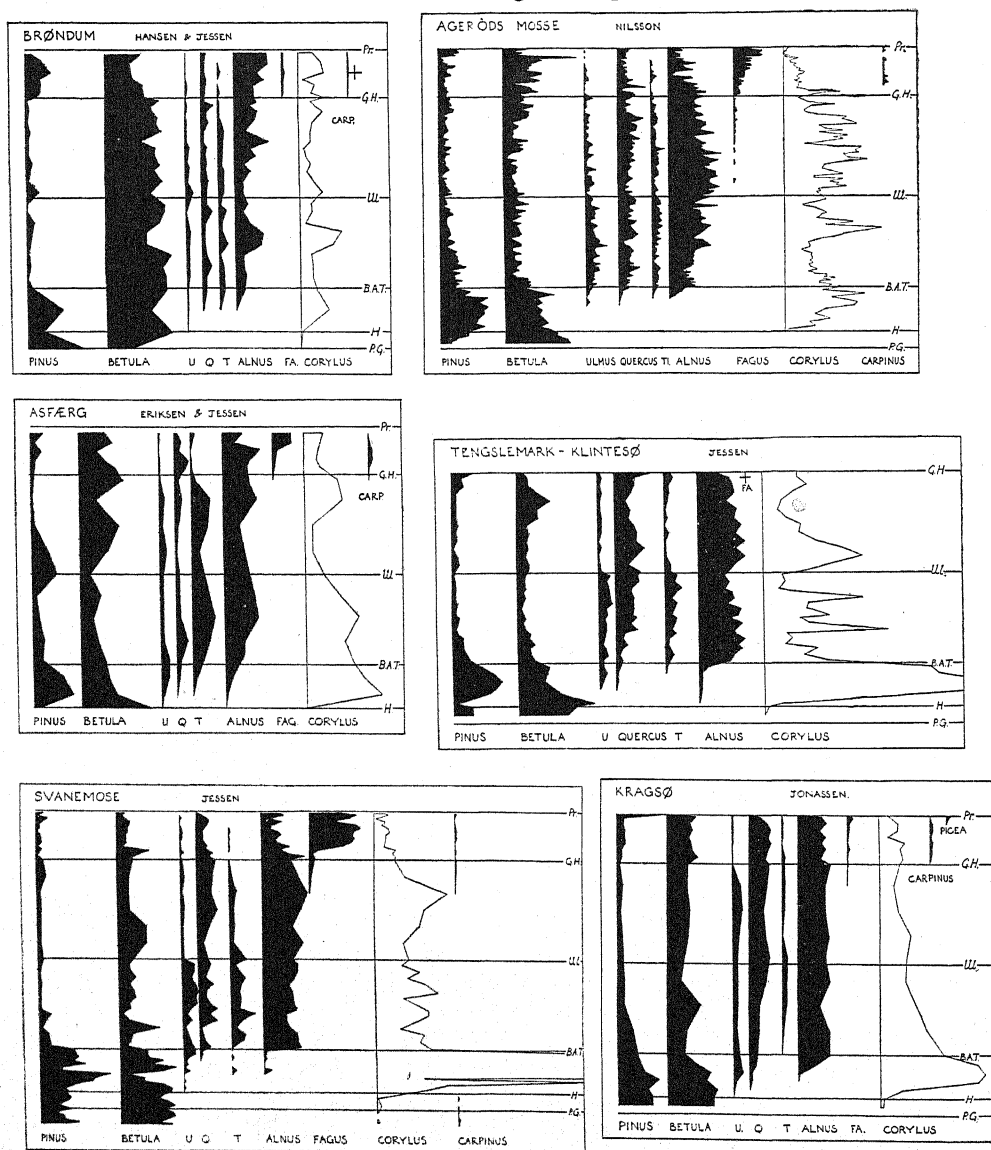
Fig. 5. Co-ordination diagram of lowland pollen series in Denmark, all reduced to a common vertical scale, with one series from south Sweden.

commented that the Brøndum diagram is abnormal in the very high values of birch, and this has caused corresponding depression in the pollen curves of the other trees and of hazel. The five Danish diagrams must of course be taken as representative of, and as linking up with, the long series of Danish diagrams already published, and through them to the many archaeological correlations established by Jessen and others. It might seem

unreasonable to regard the one figure of Ageröds mosse in the same way as representative of the south Swedish type of pollen diagram, but T. Nilsson's most elaborate and exhaustive analysis of diagrams from that region certainly justifies this, and in this region a still closer complex of archaeological correlation has been created.*

Nothing in the outcome of archaeological correlation across the north-west European coastal plain seems to forbid the conclusion that post-glacial forest history has pursued a very similar course over the whole of this region, and that the index horizons we have employed may be regarded as roughly synchronous throughout. In reaching this conclusion it will have been remarked how little comment has been made on the form of the hazel curve, and indeed no other curve shows so much variation. It is an extraordinary fact that whereas certain diagrams may show striking similarities in their *Corylus* curves, in others the discrepancy is striking; in some the hazel curve is both high and rapidly fluctuating, and in others it is low and even; in Klintesø and Svanemose there is a very big hazel maximum between *H.* and *B.A.T.*, whilst other diagrams show low maxima at this time, and others no maximum at all. We still lack explanation of such differences, but they are so familiar in all the regions considered that we acknowledge that they do not prevent correlation on the basis of the tree-pollen curves themselves.

We conclude our consideration of the pollen-historic background by reference to the synthetic pollen diagram from Dunshaughlin, Eire, produced by Mitchell (1942). This (Fig. 6) has been scaled similarly to the other west European diagrams, and will be observed not to distort the pattern they have yielded, though differing in the absence of *Tilia*, *Fagus* and *Carpinus*, in the very high values of *Ulmus*, and of *Corylus* between the *H.* and *B.A.T.* horizons. Mitchell's archaeological correlations have been included in our diagram, and these are also conformable, except that the Bronze Age falls late in relation to the *G.H.* horizon.

C. HOLLAND

In the post-glacial deposits of Holland, fresh-water peat formations and marine deposits alternate strikingly with one another, and over big areas the following sequence can be recognized:

Young sea-clay	Jonge Zeeklei	I 10 k (Dutch Geol. Survey index)
Upper peat	⎰Laagveen	I 5 v „ „ „ „
	⎱Hoogveen	I 4 v „ „ „ „
Old sea-clay	Oude Zeeklei	I 3 k „ „ „ „
Lower peat	Veen op grootere Diepte	

The general disposition of these deposits is given in Fig. 7, which is copied from Vermeer-Louman's reproduction of a section constructed by Badon Ghyton from Haarlem to Loosdrecht. From this it will be seen that the thick peat beds which form the surface of most of this section are continuous on the landward side, but on the seaward side are divided by the incursion of the fine sands and clays of the 'Old sea-clay'. Thus we have distinguished clearly the 'oppervlakte veen' from the 'veen op grootere diepte'. Thanks especially to Vermeer-Louman we have the means of pollen-analytic dating of these peat

* It should be noted that Nilsson considers a small section of the Ageröds mosse profile to be absent, thus giving a discontinuity about the *B.A.T.* level. We have disregarded this gap in making our diagram. In the Brøndum profile an archaeological correlation is provided by the find of a Late Bronze Age vessel at the *G.H.* level.
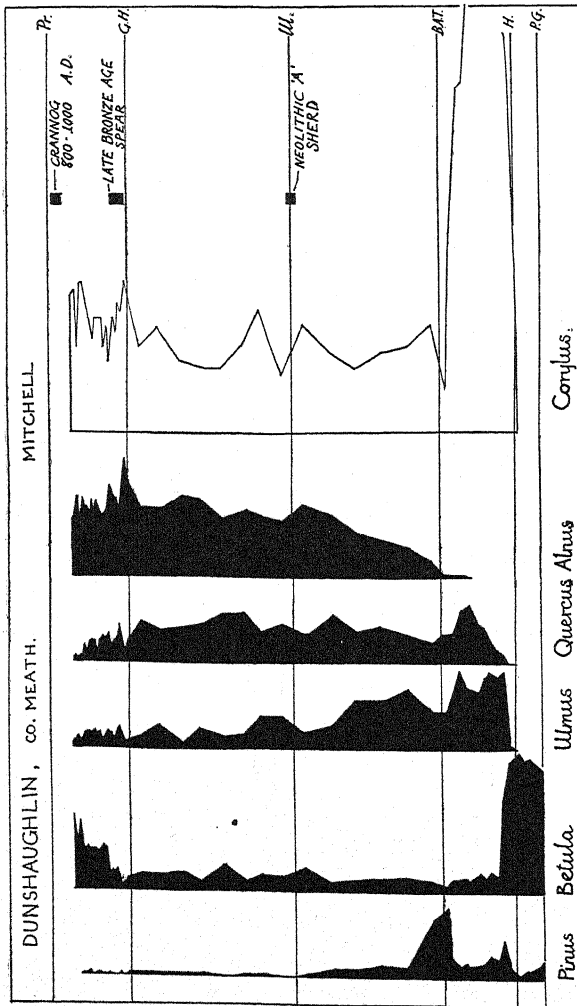
Fig. 6. Synthetic diagram from Eire, after Mitchell, reduced to the common vertical scale used in Figs. 2–5.
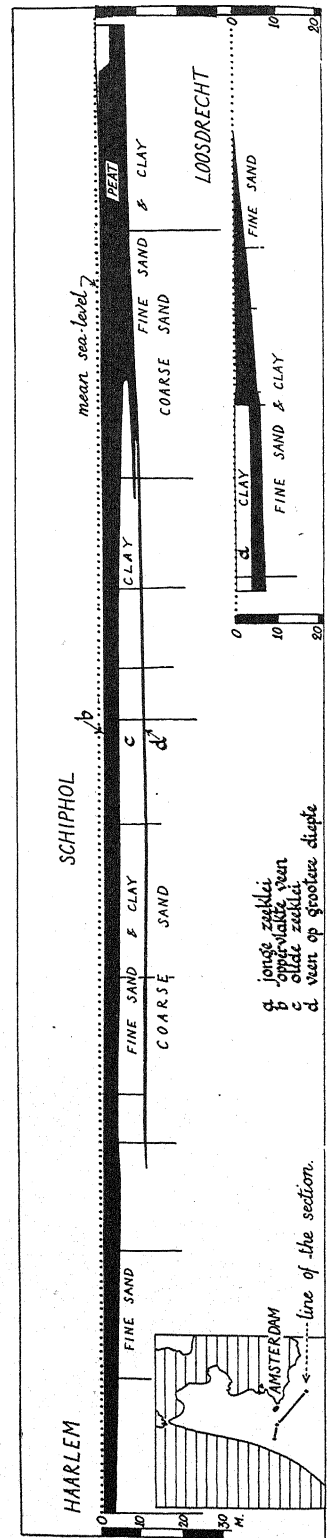
Fig. 7. Profile through Dutch lowland marsh deposits, after Vermeer-Louman.

beds in their various occurrences, and it should be noted in passing that by pollen analysis Vermeer-Louman easily distinguishes between these post-glacial peats and the inter-glacial peats associated with the Eem Sea beds, which also occur at no great depth in the neighbourhood of Amsterdam. Pollen analyses have been made of the 'veen op grootere diepte' at a large number of sites, but as the peat is generally encountered in borings, only isolated analyses are, as a rule, available. It is pointed out by Vermeer-Louman that the sites where this peat is deepest lie to the west, and that there the peat is older, whereas the less deep peat in the east is younger, as if formed later in the course of marine trans-gression. The results of consideration of these analyses are presented in Table 3.

It appears from these data that depths as great as 37 m. (122 ft.) were above sea-level in zone VIc, but that sea-level had risen by the time of transition to zone VII (i.e. *B.A.T.* horizon) to 22 m. if we judge from Wijk aan Zee, or to 12 m. if we judge from

Table 3. *Peat beds analysed by Vermeer-Louman*

Boring no.	Title	Depth in m. below sea-level	Reference to English zone	Remarks
1	Wassenaar	17·2	VIc	
2	Meyendel	16·0	VIc	
3	Leiden	16·7	VIb–VIc	
4	Loosduinen	15·0–16·0	? VIc	
5	Bennebroek	14·1	VIc	
6	Uithuizen	17·0	VIc	
8	Purmerend	?	VIc	
9	Beverwijk	20·0	VIc and VIIa	
10	Wijk aan Zee	22·0	VIc and VIIa	Transition to humous clay near *B.A.T.*
11	Bergen	23·6	VIIa	
13	Wormebeer	17·8	VIc	
14	Haamstede	37·2	VIc	
16	Rotterdam	16·0–17·0	VIc and VIIa	
17	Leiden	14·7	VIIa	
18	Bergen	9·3	VII	
19	Leijmuiden	11·6–12·0	VIc–VIIa	Marine contact above peat near *B.A.T.*
21	Hemburg	12·4	VIIa	Clay above, sand and peat below
27–45	Amsterdam—Uithoorn	9·5–11·6	VIc–VIIa	

Leijmuiden.* It is evident that the last stage of transgression was rapid and extensive in the last part of zone VIc. Vermeer-Louman groups together all the peats from a depth of more than 15 m. and regards them as falling within the period preceding domination by the Mixed-Oak forest, those of higher level being uniformly later, but this seems to ignore minor inconsistencies. It is relevant to recognize that the deep-lying peat is eutrophic in character, derived from reeds, sedges, ferns, and fen-wood vegetation, and it often lies upon a rather flat surface of sandy clay with marine shells, so that one might reasonably expect that this lower peat actually took its origin under the influence of rising sea-level, either upon the first thin marsh deposits in phases of relative stability, or directly upon older ground as a result of the enforced waterlogging and worsening of drainage.

* It is as well to notice that there are certain other difficulties in reconciling the evidence of this table. Thus, whilst it appears from boring 19 that by the time of transition VIc to VIIa the sea-level had reached approximately −12·0 m. N.A.P., from boring 11 it would seem that still in zone VIIa, for peat to form, the sea must have been more than 23·6 m. beneath N.A.P. The peat in boring 14 also is very late by pollen-floristic dating (VIc) for so great a depth as 37 m. below sea-level: though this dating is not directly opposed by any evidence in the table, it hardly accords with data from the German coast (see p. 45). It is not possible to say how far factors such as erosion, transport, compression and slipping may be responsible for such effects, or how far, alternatively, interpretation of the pollen-analyses may be incorrect.

It is of particular interest to consider a longer pollen diagram from a profile passing through the deep-lying peat. This is given by Florschütz for Rotterdam, where, as is shown in Fig. 8, the deep peat lies about 15·5 m. below sea-level and gives place to the Old Sea-clay at a stage in forest history which must be very close indeed to our *B.A.T.* horizon. A very similar conclusion is given also by consideration of the long profile from Wieringermeer Polder (Vermeer-Louman, p. 132), where the base of the Old Sea-clay is about −7·8 m.
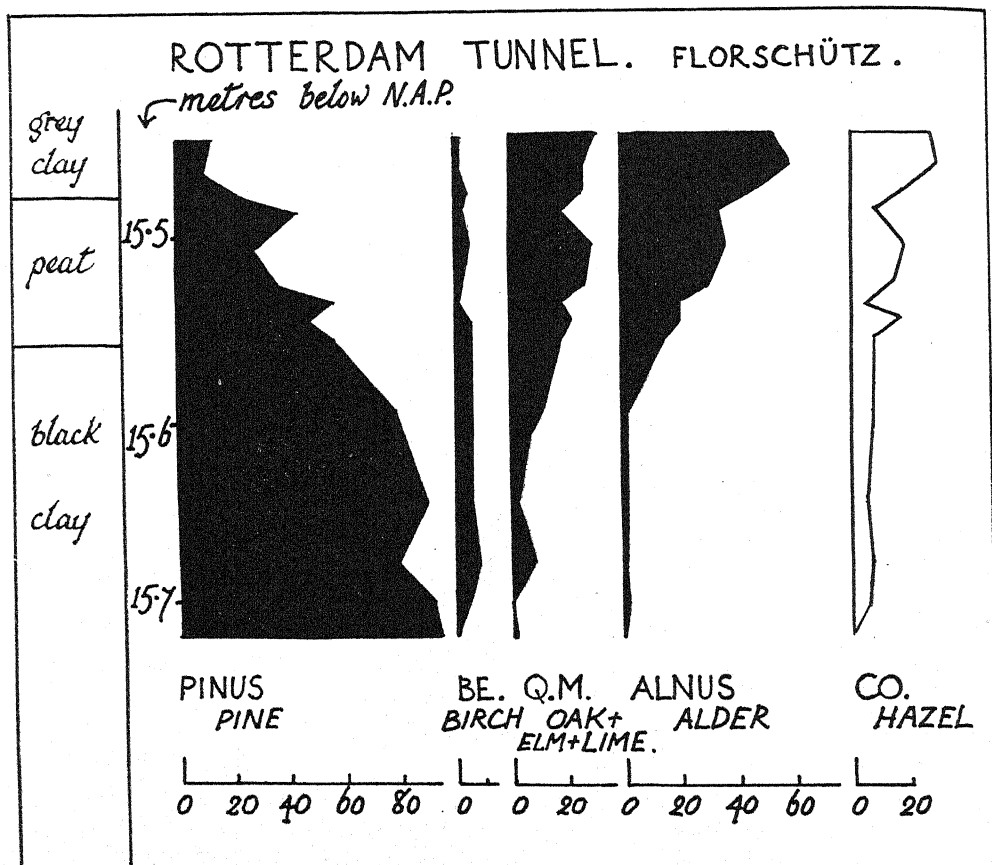
Fig. 8. Pollen diagrams indicating at least 15 m. submergence since time of replacement of pine dominance by that of alder and mixed-oak forest.

From the foregoing we learn of the onset of the Old Sea-clay: what we next require to know is the duration and vertical extent of the transgression. It appears from the Haarlem-Loosdrecht section that the present surface of the Old Sea-clay is about 5–6 m. below sea-level, and a detailed profile by Vermeer-Louman (Fig. 9) gives us the opportunity of dating the upper clay surface pollen-analytically. In the same profile at a depth of 11 m. was the deep-lying peat beneath the Old Sea-clay. The *Grenzhorizont* lies at −2·8 m., and below this is 0·8 m. of the Old *Sphagnum* peat, itself overlying *Carex* and *Phragmites* peat. The replacement of *Quercus* and *Pinus* dominance by that of *Alnus* in the lower samples can scarcely be attributed to the *B.A.T.* transition period, for beech

and spruce pollen are too abundant, and though the evidence is inconclusive it appears highly likely that the sea-clay phase ended in the middle of zone VII.

The Young Sea-clay, which overlies the upper peat in some places, is referred to the marine invasions which caused formation of the Zuider Zee in the twelfth and thirteenth centuries, and pollen diagrams by Polak (1936) in the north-east polder of what was formerly the Zuider Zee show that the beech-pollen maximum occurs in the peat below
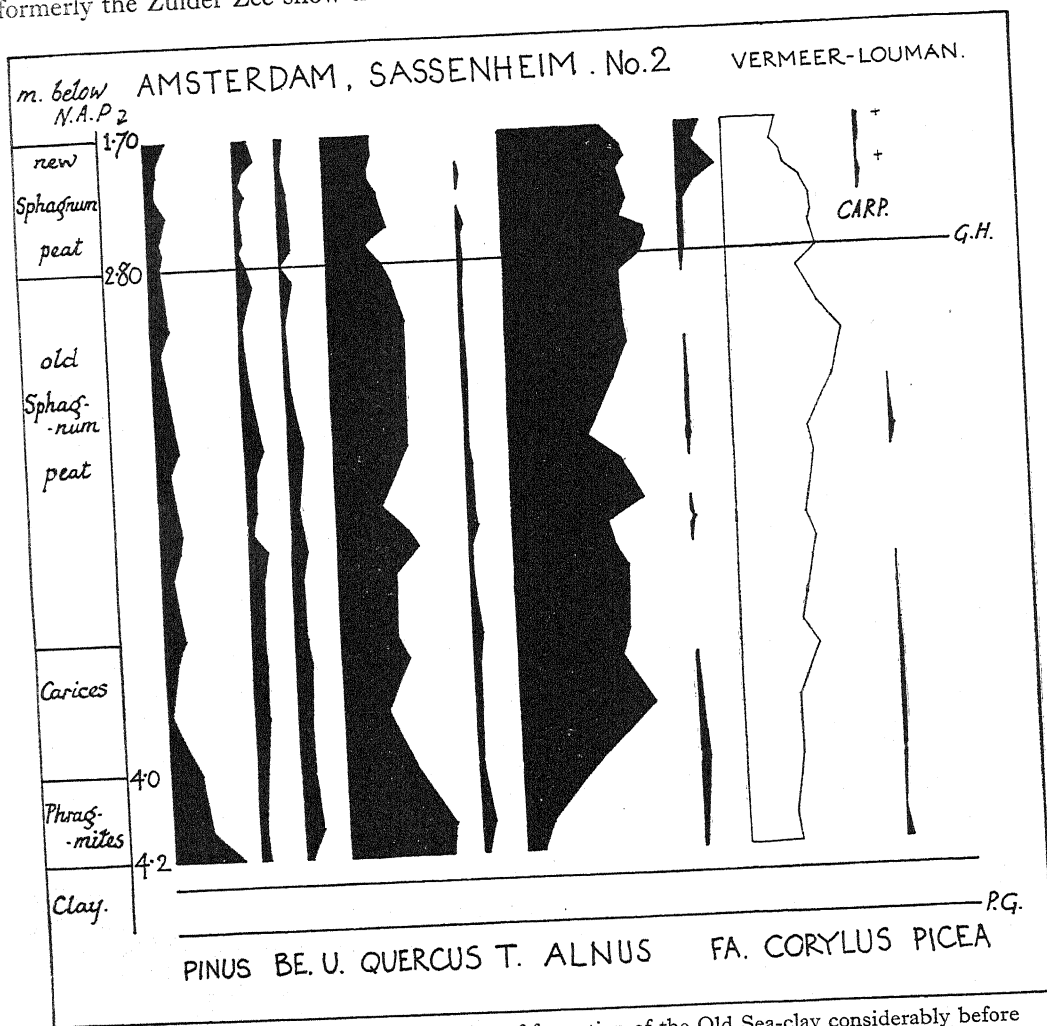
Fig. 9. Pollen diagram indicating cessation of formation of the Old Sea-clay considerably before the *G.H.* horizon, and at a depth of 4·0 m. below sea-level.

the Young Sea-clay, as would be expected on this hypothesis. Dutch geologists apparently hold (see de Leeuw, 1935) that the Old Sea-clay was laid down behind a coastal bar on which a big dune system developed, and which persisted whilst the Old *Sphagnum* peat was formed in the complex of great raised-bogs which developed on the flat clay surface. The southern part of this dune system was largely destroyed in late Roman days (A.D. 300–500), and after about A.D. 900 a new extensive dune system arose, although it did not prevent the culmination of destruction which finally led to the formation of the

Zuider Zee. The development of these dune systems is apparently accepted as sufficient cause to account for the development of the thick *Sphagnum* peat between two marine layers, without recourse to invoking a period of relative emergence of the coastline to break the progress of a continuously rising sea-level. We may, all the same, doubt whether, in view of evidence from Germany and the English Fenland, such temporary marine retrogression was in fact absent.

D.   German North-Sea coast

Between the Dutch frontier and Schleswig-Holstein is the low coastline of north-west Germany, where the characteristics of a recently submerged coast are apparent in the wide and shallow embayments of the Dollart and the Jade Bucht, with the long estuaries of the Weser and the Elbe, as well as in the nature of the chain of the East Friesian Islands continuing the line of the outer Dutch coast. The great ports of Hamburg, Bremen, Wilhelmshaven and Emden occur within this short, one hundred miles long stretch of coast-line, and sufficiently explain the desirability to the German scientist of learning at once something of the stratigraphy of this district and of the history of the land-and sea-level changes which have so much determined its structure. Foremost to develop these studies has been H. Schütte (1935), most of whose life has been given to 'Marschen-geologie', and whose conclusions strongly assert the intercalation of three periods of elevation in the general progress of submergence of this coast. Critics have not been lacking, and to the complex field of this inquiry, pollen analysis and bog stratigraphy offered welcome promise of general correlation indices. In the last twelve years or so, there have in consequence been published a series of pollen-analytic investigations directly aimed at elucidating the structure and history of different portions of this coast-line. This series was produced by students working with F. Overbeck at Frankfurt, and appears as successive contributions 'Zur Geschichte der Moore, Marschen und Wälder Nordwestdeutschlands':

    I.   Niederweser und unter Ems, by Overbeck and Schmitz.
   II.   Oste und Niederelbe, by Schubert.
  III.   Jade, by Brinkmann.
  IV.   Nordfriesland, by Ernst.
  VI.   Lüneberg und Bremen, by Overbeck and Schneider.

(For full titles see References, p. 68.) In 1934 the publications which had then appeared were summarized in a very concise and satisfactory fashion by Overbeck, and we cannot do better than follow his sequence of treatment.

With regard to the deep moorlog peats of the North Sea floor it will suffice to recall that we have already indicated that most samples are referable to zones IV and V, the periods of birch and pine dominance, and that some samples from about 19 fathoms (35 m.) are referable to zone VI *a*, in which oak begins to expand and hazel reaches high values (Godwin, 1943). None of the deep submerged peat seems to be later than this. The conclusions of Overbeck and of Jessen (1935 *a*) accord with this view.

Next to be considered is a series of dredger samples from the Jade Bucht and Weser estuary, analysed by Erdtman (1927) and by Overbeck & Schmitz (1931). Their results are given in Table 4. They all come from between 10 and 20 m. beneath present sea-level. A few samples are earlier, but it will be apparent that most were formed at a time when,

although pine maintained substantial values, the Mixed-Oak forest trees were present in strength, and the alder had become numerically preponderant. That is to say, peat formation clearly continued, at these levels, above the *B.A.T.* horizon into zone VII. Erdtman wrote of some of the samples as 'Atlantic or younger', but we must agree with Overbeck that the total absence of *Fagus* from these samples (as well as the high pine values) makes it unlikely that they relate to anything but the early half of the period, that is, to the early part of zone VII.

Evidence of the interplay of marine and fresh-water conditions at somewhat higher levels is provided by the work of Wildvang on the East Friesian marshes between Dollart and the Ley Bucht (Wildvang, 1933). His diagrammatic profile through these marshes (Fig. 10) discloses a sequence resembling that given for the Dutch coast: landwards there is a single peat bed, but seawards it is split into two by marine clay, and is also overlaid by clay. Pollen analyses made at Langeoog, Norderney and Pilsum respectively indicate the progress of the submergence responsible for the lower clay. The thin lower peat at Langeoog, now 19·5 m. below sea-level, was formed close to the *B.A.T.* horizon. At Norderney the peat is between 11·5 and 11·0 m. deep, and though almost 50 cm. thick,
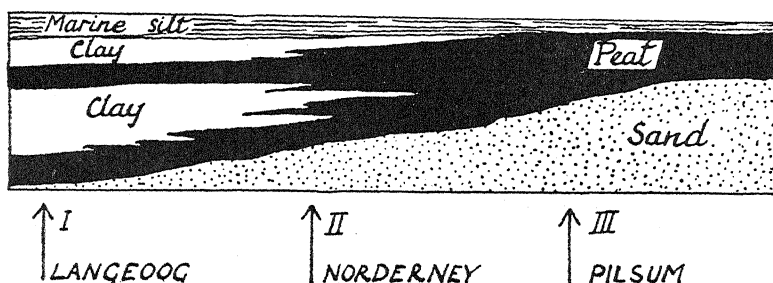
Fig. 10. Diagrammatic section through the East Friesian coastal marshes (after Wildvang).

the *B.A.T.* horizon is near its base, showing that whilst peat formation began at the same time here as at Langeoog, it continued longer at the landward site until brought to an end by the marine incursion. At Pilsum the base of the peat is at −7·5 m., and is of the same age as at the other sites, but here peat formation has continued much later, being indeed stopped only by a transgression later than that which affected Langeoog and Norderney (Fig. 11).

These results confirm the results of the dredging analyses, that early in zone VII*a* marine transgression reached levels now about 19 m. below sea-level. Sites farther inland may be instanced to indicate the later progress of the same transition: data are plentiful, but we shall follow Overbeck in citing only the most informative of them.

From Hooksiel on the west side of the Jade Bucht, Overbeck & Schmitz (1931) have given pollen analyses of peat at three different levels (Fig. 12). The lowest peat is clearly interglacial, for it has values of hornbeam and spruce pollen never found in west European post-glacial sequences. The middle peat is now between 12 and 14 m. beneath sea-level. In its lowest layers it is an organic mud from the period of birch, pine and willow dominance, but its middle layers show the expansion of the warmth-loving trees, and in the *Phragmites* peat at the top, the pollen spectrum has 56% of alder, and apparently corresponds to the youngest of the dredger samples already mentioned, and constitutes

Table 4

Site	No.	Depth below sea-level, m.	Peat type	Pi.	Be.	Ul.	Q.	Ti.	Al.	Fa.	Ca.	Pe.	Co.
Weser estuary dredging	I 1	11·5–12·0	Wood peat	28	7	9	6	18	31	—	—	—	7
	II 2	11·5–12·0	„	60	16	—	8	2	14	—	—	—	24
	3	11·5–12·0	„	48	4	—	8	2	36	—	—	2	12
	III 4	11·5–12·0	„	32	4	3	3	3	55	—	—	—	26
	5	11·0–12·0	„	46	12	3	6	1	31	—	—	—	14
	6	11·0–12·0	„	51	12	4	9	1	23	—	—	—	5
	7	12·0–12·5	*Phragmites* peat	19	3	1	6	4	65	—	—	—	19
	IV 8	12·0–12·5	„	45	9	2	3	2	38	—	—	—	14
	9	12·0–12·5	Clayey mud	39	15	1	2	4	56	—	—	—	22
	V 10	12·0–12·5	Wood peat	20	19	1	2	2	58	—	—	—	41
	VI 11	12·0–13·0	*Phragmites* peat	23	8	2	8	1	58	—	—	—	25
	12	10·0	„	29	12	1	6	2	49	—	—	—	29
	13	10·0	„	13	39	4	6	1	37	—	—	—	13
	VII 14	10·0	„	37	17	1	5	3	37	—	—	—	31
	15	10·0	„	37	14	0	3	7	39	—	—	—	40
Wilhelmshaven harbour mouth dredging	I	c. 15·0	*Phragmites*+mud	9	1	3	2	—	85	—	—	—	21
	II	c. 15·0	„	11	5	4	3	4	72	—	—	—	27
	III	c. 15·0	„	17	10	2	2	5	65	—	—	—	32
	IV	c. 15·0	*Phragmites* peat	23	5	3	9	2	58	—	—	—	26
	V	c. 15·0	Rootlet peat	13	18	2	9	1	56	—	—	—	29
	VI	c. 15·0		31	11	4	9	2	43	—	—	1	25
Jade Bucht and Weser estuary dredging	1	16·0	—	27	73	—	—	—	—	—	—	—	3
	2	14·0	—	88	12	—	—	—	—	—	—	—	56
	3	12·0	—	46	50	4	?	—	6	—	—	—	6
	4	17·0	—	43	51	—	—	—	18	—	—	—	24
	5	17·0	—	68	14	—	14	+	30	—	—	—	24
	6	14·0	—	22	30	4	12	—	53	—	—	—	14
	7	17·0	—	12	20	3	20	—	39	—	—	—	22
	8	17·0	—	12	22	6	8	1	56	—	—	—	6
	9	19·0	—	11	24	1	17	—	40	—	—	—	13
	10	17·0	—	10	24	6	8	3	62	—	—	—	16
	11	14·0	—	9	18	3	16	—	46	—	—	—	44
	12		—	8	25	4		1		—	—	—	
Kongedyb	—	13·0–15·0		13	78	4	2	1	1	—	—	—	58
Fil Sö	—	6		31	12	6	14	2	30	—	—	2	14
Kåseberga	1	37	—	68	10	4·5	1·5	1	11	—	—	2	16
	2	59	—	95·5	4·5	—	—	—	—	—	—	—	—
S.E. of Bornholm	—	13·0–15·0	—	78	13	4	2	1	1	—	—	—	58
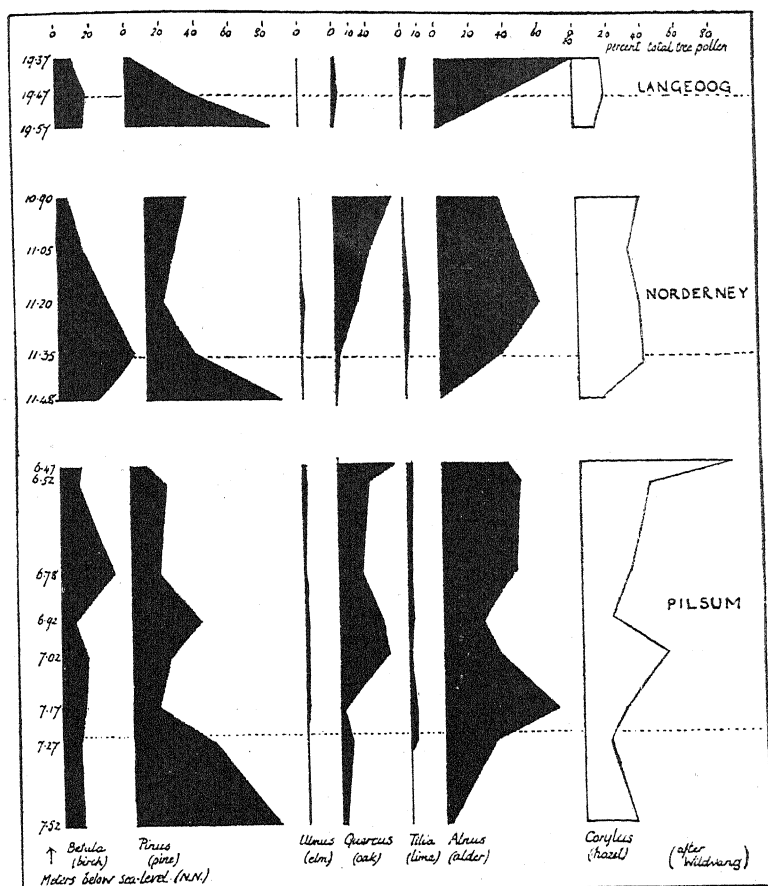
Fig. 11. Pollen diagram in the East Friesian marshes, showing that in landwards and seawards sites alike peat formation began at the same time, but continued much later in the landward sites where marine transgression was effective later.
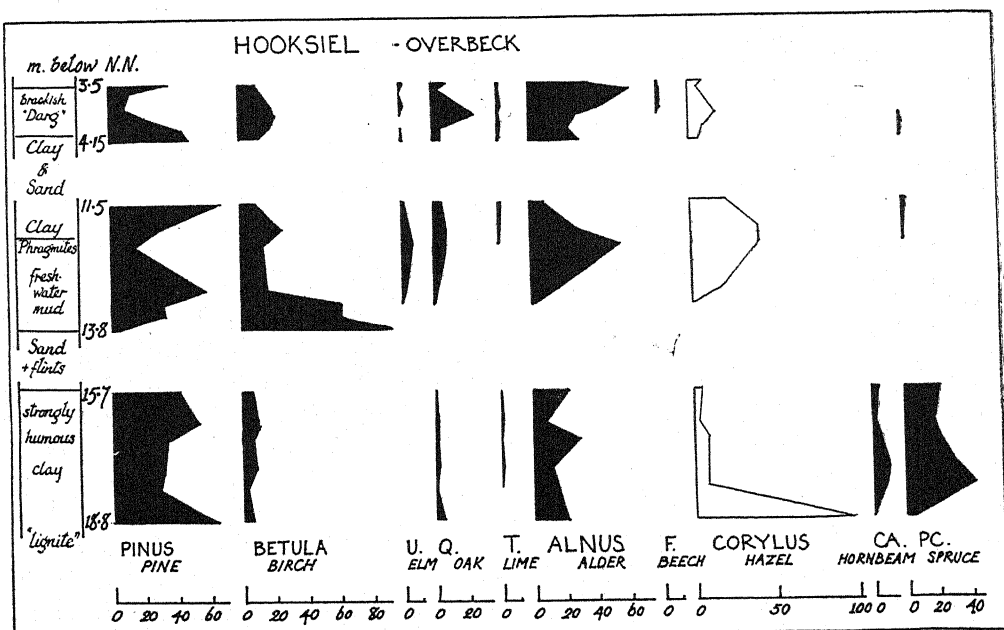
Fig. 12. Pollen diagram from Hooksiel. The lowest peat bed is interglacial. The middle formed at the time of the *B.A.T.* horizon, and indicates a subsequent submergence of more than 13 m.

evidence that peat formation at − 12 m. was brought to a stop by marine transgression early in zone VII. Much higher in the profile brackish-water *Phragmites* peat (*Darg*) yields a pollen profile containing beech, but not otherwise of very distinctive character.

Two extremely valuable profiles have been given by Overbeck's pupil, Brinkmann, from the bogs at Sehestedt and Mentzhausen, on the east and south-east side of the Jade Bucht. In both the uppermost layers are the Fresh *Sphagnum* peat; this is succeeded downwards by the Old humified *Sphagnum* peat, by wood peat and by *Phragmites* peat, which then gives place to thick marine deposits of clay; below these again are fresh-water layers. The detailed pollen profiles are given in Figs. 13 and 14. At Sehestedt the lower peat is
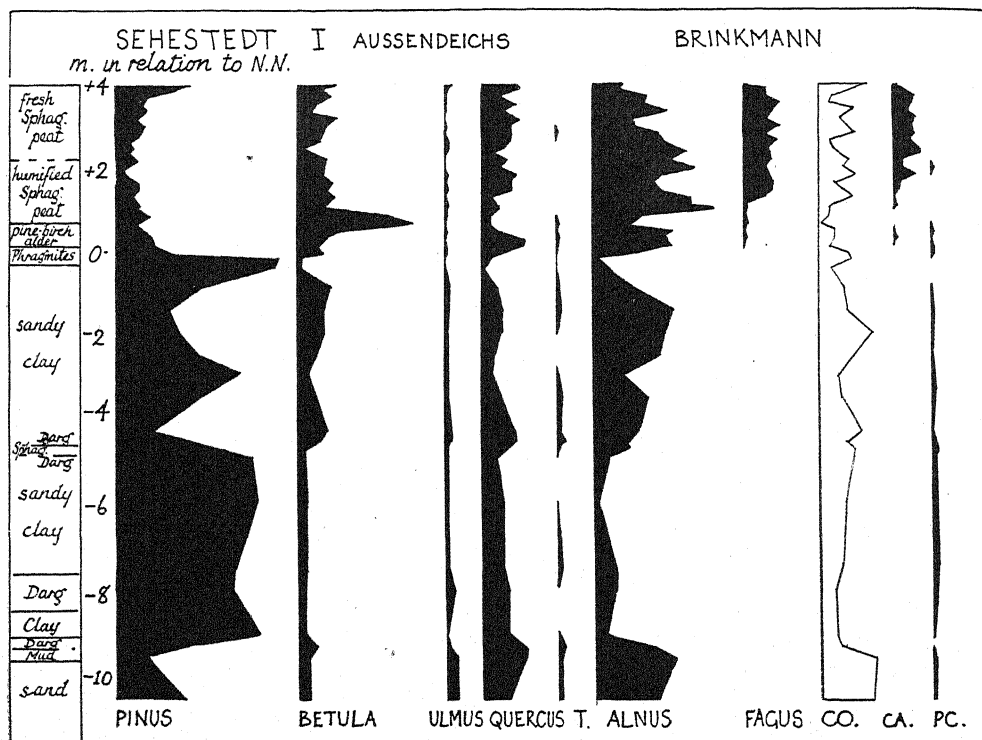
Fig. 13. Profile from Sehestedt showing interplay of marine and fresh-water conditions between sea-level and − 10 m., and above sea-level a transition to raised-bog, which indicates freedom from marine influence in a period extending over the *G.H.* horizon.

a muddy humified peat, now about 9·2 m. below sea-level, and with a pollen spectrum clearly referable to a time after the *B.A.T.* horizon. The *G.H.* level is indicated stratigraphically, and below it is 1·5 m. of the Old *Sphagnum* peat as well as wood peat, *Phragmites* peat and the marine layers, so that we can evidently assume the bottom of this peat to have formed fairly early in zone VII. The upper surface of the marine deposits now lies at sea-level: above it the beech pollen curve is continuous, and both this and the thickness of the Old *Sphagnum* peat indicate that the marine transgression ended a long while before the *G.H.* horizon. In this diagram, as in the next, the high pine values in the marine clays must be discounted as due to over-representation by some unknown means: this phenomenon is common throughout the German, Dutch and English coastal deposits (see Brinkmann, 1934; and Godwin, 1943). At Mentzhausen the thick organic

mud (nekron mud) at the base of the section is succeeded by wood peat, and then by oligotrophic raised-bog peat, before the onset of the marine deposits at about 7 m. below present sea-level. As at Sehestedt, the peat below the marine clay must be but little later than the *B.A.T.* horizon, but the top of the marine clay is possibly younger here than at Sehestedt, since only a small thickness of peat lies between it and the *Grenzhorizont*.

The evidence thus far quoted is substantially that also considered by Overbeck, who summarizes as follows: 'Es liegen eine ganze Reihe von Einzeldatierungen vor, die sich alle zu einem einheitlichen Gesamtbild zusammenfügen. Nach diesem hat die allgemeine
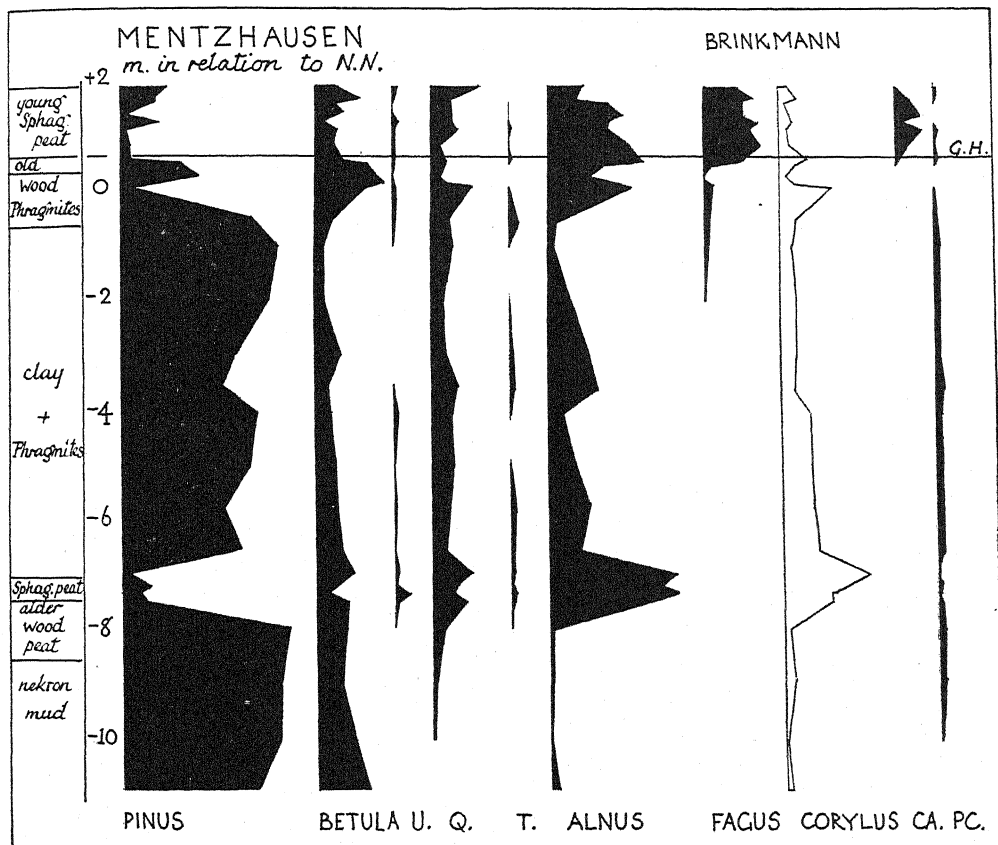
Fig. 14. Profile from Mentzhausen. The lower fresh-water beds, now 7–10 m. below sea-level, formed before the *B.A.T.* horizon. Thereafter marine beds supervened. Marine retrogression is indicated later again by raised-bog deposits at a time including the *G.H.* horizon.

Kleiablagerung im Gebiet der Jade und Weser zwischen 6,000 und 5,000 v. Chr., d. h. um die Wende vom Boreal zum Atlanticum begonnen. Dabei sind die weiter landein-warts gelegenen Moore (Oldenbrook, Mentzhausen) im frühen Atlanticum, die weiter seewärts gelegenen schon im späten Boreal in den Bereich der Überflütung eingerückt.' This is the conclusion we have already stated, though without committing ourselves necessarily to accept the dating of between 6000 and 5000 B.C. for the Boreal-Atlantic transition, our *B.A.T.* horizon.

At sites farther inland marine transgression affected peat formation differently. Thus at Bremer Blockland a thin clay bed overlies a thick deposit of fen and wood peat, which

Overbeck reasonably suggests was produced in fresh-water conditions but influenced by a rise in ground-water level caused by the marine transgression. This topogenous peat formation began in zone VI and continued long after the *B.A.T.* horizon: it ceased, however, before the *G.H.* horizon with the deposition of a thin clay layer. The onset of this clay is evidently late, Overbeck suggesting not earlier than 3000 B.C. A similar kind of evidence is provided by Schubert from Ostetal, near Bremervörde, where the following profile is given:

     (*g*)   0–40 cm.   Disturbed ground.
     (*f*)   40–95 cm.   'Knick'—decalcified dark tidal mud with *Phragmites*.
     (*e*)   95–165 cm.   *Eriophorum-Sphagnum* peat.
     (*d*)   165–175 cm.   Birch-wood peat.
     (*c*)   175–315 cm.   *Phragmites* rootlet peat with local strong clay admixture.
     (*b*)   315–445 cm.   *Sphagnum-Eriophorum* peat, strongly humified.
     (*a*)   445–475 cm.   Coarse marine sand.

It will be observed that twice ombrogenous peat formation has been interrupted by rising water-level. The first occasion gave rise to 1·4 m. of clayey *Phragmites* peat, and the pollen analyses indicate that it formed 'towards the end of the Old *Sphagnum* peat period', and we may reasonably expect that it corresponds with the onset of clay deposi-
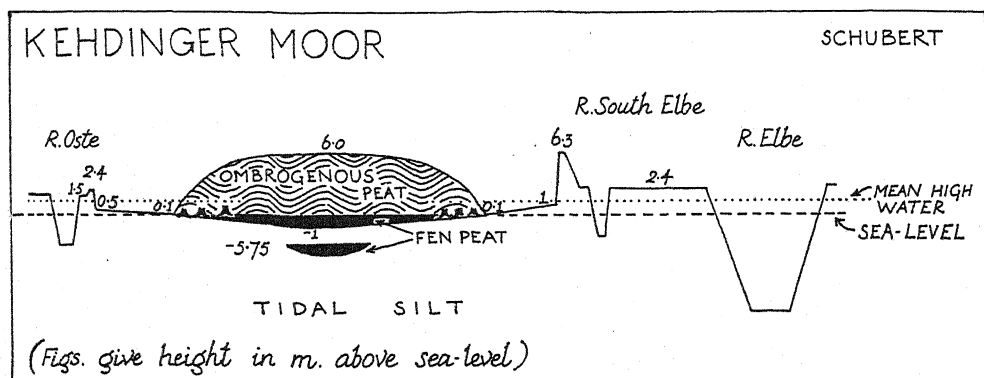
Fig. 15. Diagrammatic section through Kehdinger Moor (after Schubert). The development of this great ombrogenous bog over tidal silt is indicative of marine retrogression.

tion in the Bremer Blockland. If this is so, it must be clear that the rate of marine transgression fell off very greatly after the beginning of zone VII: during zone VI *a* the sea-level rose many metres, but in the much longer period following, until Ostetal and the Bremer Blockland were affected, far less rise was accomplished. It is indeed probable that a phase of marine retrogression may, as Schütte suggests, have intervened.

    The late stages of marine transgression are considerably illuminated by the evidence of Schubert (1933) from the big Kehdinger Moor which lies between the rivers Oste and Elbe. From this moor come the profiles 'Wolfsbrucher Moor' and 'Öderquarter' illustrated in Figs. 16 and 17. Schubert's diagrammatic transect of the Kehdinger Moor (Fig. 15) shows that it is a deep raised-bog, the ombrogenous peats of which are separated, at about mean sea-level, by a wood layer from the underlying fen peats. The latter extend to about 1 m. below sea-level, where they rest upon deep deposits of marsh clay, deposits which, however, at about −3·75 m. contain a further thin layer of peat. The oldest

pollen spectra from the clay extend back to zone VI, as one would expect from the results in the Weser estuary. The Wolfsbrucher profile (Fig. 16) shows that almost a metre of the Old *Sphagnum* peat, as well as *Phragmites* peat, overlies the silt surface, so that the end of silt deposition must have been considerably before the *G.H.* time. The bed of *Phragmites* peat, from −2 to −4 m. depth, must be correspondingly older: it presumably may represent the interruption of marine transgression already mentioned. Öderquarter (Fig. 17) yields a pollen diagram very similar to that of Wolfsbruch, so that although the *G.H.* is not directly recognizable in the stratigraphy, the diagram strongly suggests that
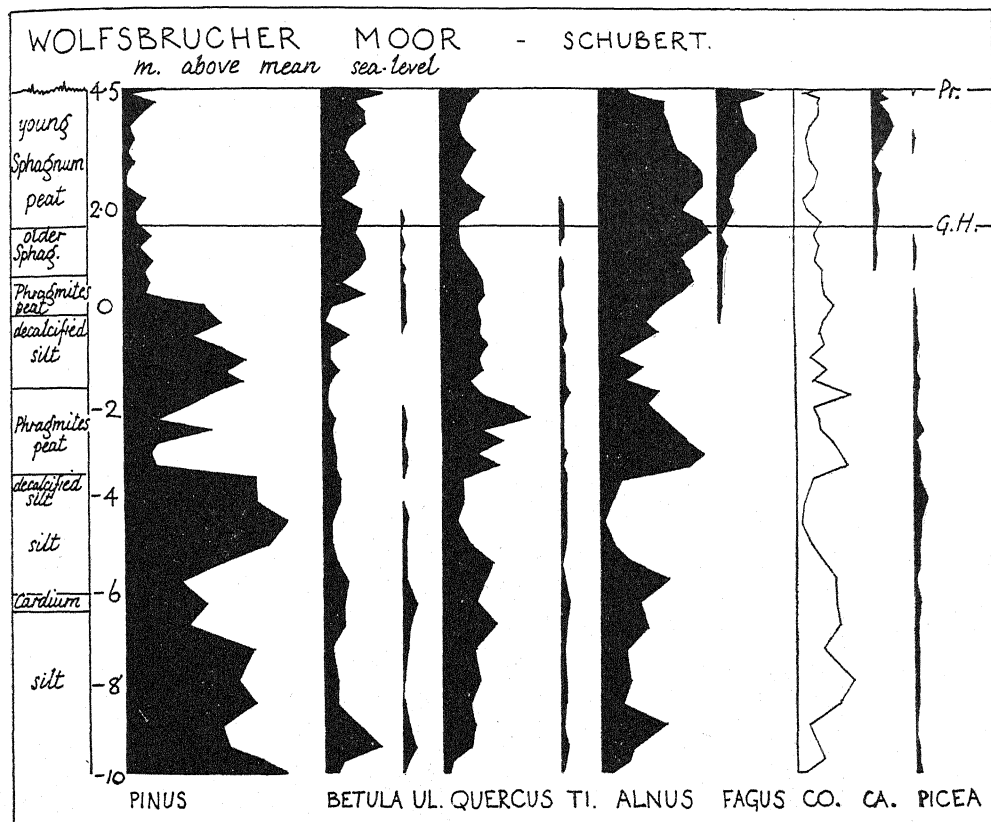
Fig. 16. Profile through the Kehdinger Moor at Wolfsbruch, showing that formation of eutrophic and then oligotrophic communities took place at about present sea-level, and before the *G.H.* horizon.

clay formation (with its transition through *Darg*, *Phragmites* peat, and sedge peat to fresh *Sphagnum* peat), ends at the same time in both parts of the moor. In the extensive development of oligotrophic plant communities from fen all over Kehdingen at the same time, Schubert sees clear evidence for marine retrogression, and as he dates the transition to raised-bog at about 1800–1600 B.C., this agrees pretty well with Overbeck's estimate for the end of clay formation in the Jade district as between 2000 and 1000 B.C. These dates are of course only rough and provisional. Evidence of marine retrogression was produced earlier by Schütte from the sequence of deposits at the marine observatory at Wilhelmshaven (Overbeck & Schmitz, 1931). The observatory rests on the clay and dung layers of one of the 'Wurts' so common upon the German coast: hillocks which served

as dwelling sites for Roman and post-Roman inhabitants of the low coastal marshes, and which were constantly and deliberately raised in level by their occupants to keep their dwellings above the wet tidal land. The bottom of the wurt rests upon peat, the top of which consists of a thin, but unmistakable layer of *Sphagnum* peat. Beneath, the peaty clay extends downwards to meet the basal wood peat and *Phragmites* peat at about 12 m. below present ground-level. Not only does the *Sphagnum* peat itself show freedom from marine influence, but directly upon it are the potsherds of an occupation datable to about
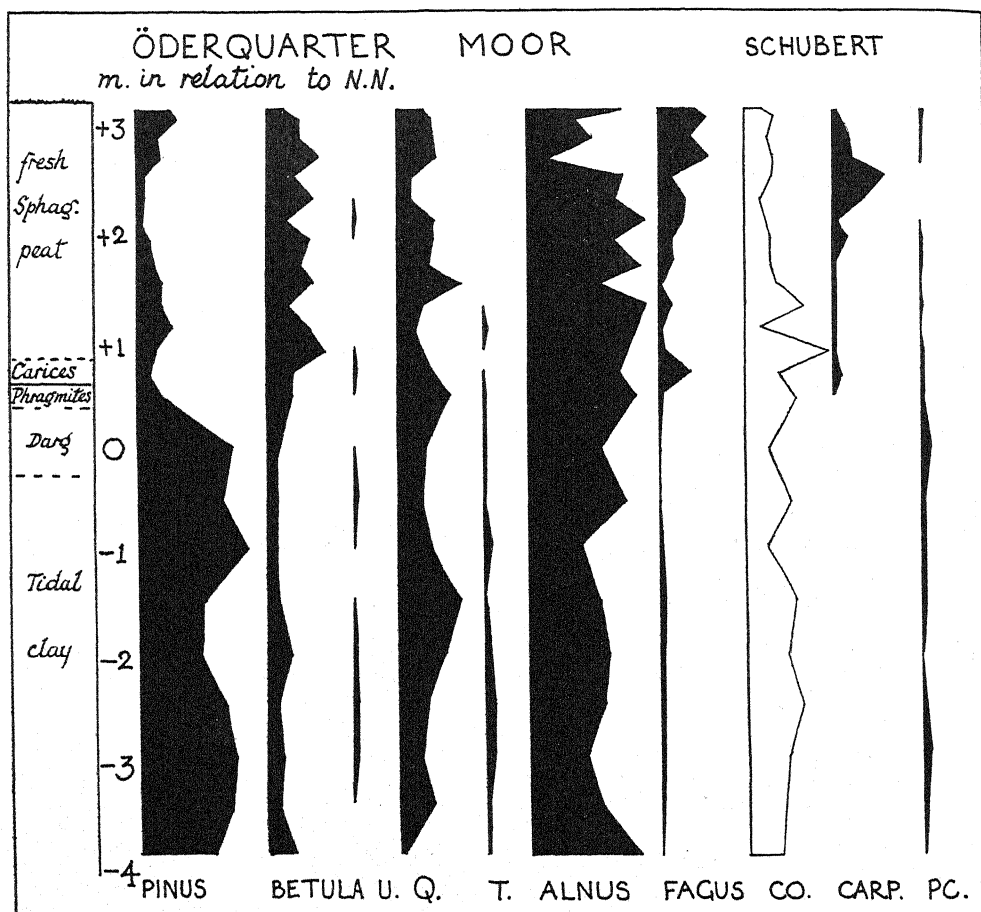
Fig. 17. Profile through the Kehdinger Moor at Öderquarter, showing transition from tidal to oligotrophic and eutrophic conditions at about present sea-level. The Old *Sphagnum* peat is missing, and the transition may therefore be later than at Wolfsbruch (see Fig. 16).

A.D. 300; an occupation made without need for any artificial raising of ground-level. This evidence is used by Schütte to demonstrate and date his third 'Hebungsperiod', and to illustrate the sinking which succeeded it. It is pointed out by Overbeck that the thinness of the peat and the date of the Roman remains above it suggest either that the upper layers have been removed during the occupation, or that we must suppose the marine retrogression to have been much later here than at many sites not far distant.

Further evidence of the retrogression is furnished by Wildvang (1934–5 a, b), particularly from the two sites of Woltzeten and Uttum. At Woltzeten, near Pewsum (Fig. 18),

between two layers of tidal clay is a peat deposit 0·7 m. thick, which consists of the following layers in sequence from below upwards: *Phragmites* peat, fen-peat, Old (humified) *Sphagnum* peat, Young (fresh) *Sphagnum* peat. Between the two ombrogenous peat layers is a clear boundary, which is regarded as equivalent in age to the *Grenzhorizont*. This interpretation is borne out by the pollen diagram, for the *Tilia* and *Ulmus* curves cease at this level, and both *Fagus* and *Carpinus* curves extend below it. It is evident that the peat layers represent a vegetational sequence to a dry raised-bog, which could only have occurred in a phase of definite marine retrogression. Still more decisive is the evidence Wildvang produces from Uttum (Fig. 19). At this site collapse of a church wall caused investigations which disclosed the section set out below:

m. above or below sea-level	
5·5 to 5·0	Rubble
5·0 to 4·2	Introduced clay with wall debris
4·2 to 2·7	Loose graveyard soil
2·7 to −0·4	Layered dung and clay of a Warf (= Wurt)
−0·4	Level of base of Warf
−0·4 to −3·0	Blue-grey chalky tidal mud, penetrated by *Phragmites*, and below transitional to *Darg* (*Phragmites* clay), and to *Phragmites* peat
−3·0 to −3·6	Young raised-bog peat with secondarily intruded clay layers
−3·6 to −4·2	Old (humified) raised-bog peat
	Glacial sand.

Height of neighbouring land surface = −0·4 m.
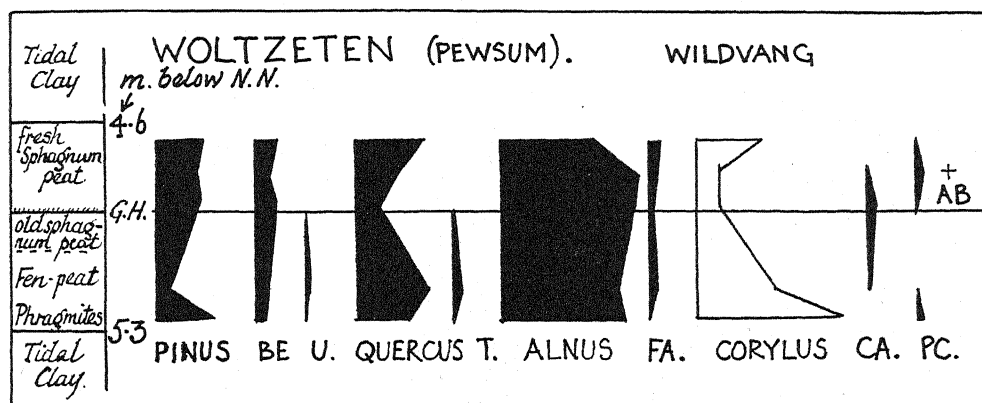
Fig. 18. Profile at Woltzeten, showing oligotrophic peats indicative of marine recession, at the *G.H.* period, between the clay deposits of preceding and succeeding transgressions. (*N.N.* = normal null = mean sea-level.)

Unfortunately there are no datable sherds in the warf dung and clay, but in two other warfs close by, at comparable levels in relation to Normal Null, abundant evidence was present of origin in the first century A.D. The base of the warf in the three given instances lies at 0·0 m., −1·2 m. and −0·4 m., and it appears that the warfs were built up in response to tidal flooding during coastal sinking which persisted through the early centuries of the Christian era. The general land surface was colonized towards the end of the 9th century. As will be seen from Fig. 19, not only is the *Grenzhorizont* evident stratigraphically, but its dating is confirmed by the drift of the pollen curves. It seems evident that this region was too elevated to be within reach of the earlier transgression, naturally remained free from marine influence during the retrogression which occurred over the *G.H.* period, and came under tidal influence of resumed transgression at a time just before the Christian era.

We may summarize the evidence in the following tabular manner:

(a) *North Sea.* Zones IV–V. Sea below −35 m.

(b) *Jade-Weser dredger samples.* Zone, early VIIa. Sea not yet reached −10 to −20 m.

(c) *Pilsum, Norderney and Langeoog.* Early in VIIa transgression reached −19 m.

(d) *Hooksiel.* Early in VIIa transgression reached −12 m.

(e) *Sehestedt.* Transgression going on in VII: ceased a long time before *G.H.*

(f) *Mentzhausen.* Transgression early in VIIa reached −7 m. but ceased before *G.H.*

(g) *Bremer Blockland.* Transgression only just reached here: it was late in zone VII, but before *G.H.*

(h) *Ostetal (near Bremervörde).* Ditto, but late stages of transgression were very gradual.

(i) *Kehdinger Moor profile*⎱
(j) *Öderquarter Moor*   ⎰ Clay formation ended well before *G.H.* at about
(k) *Wolfsbrucher Moor*   ⎰ present sea-level, but just before this was a short and slight retrogression.

(l) *Woltzeten.* A phase of retrogression covering the *G.H.* period.

(m) *Uttum.* Ditto, with retrogression giving place to transgression about first century A.D.
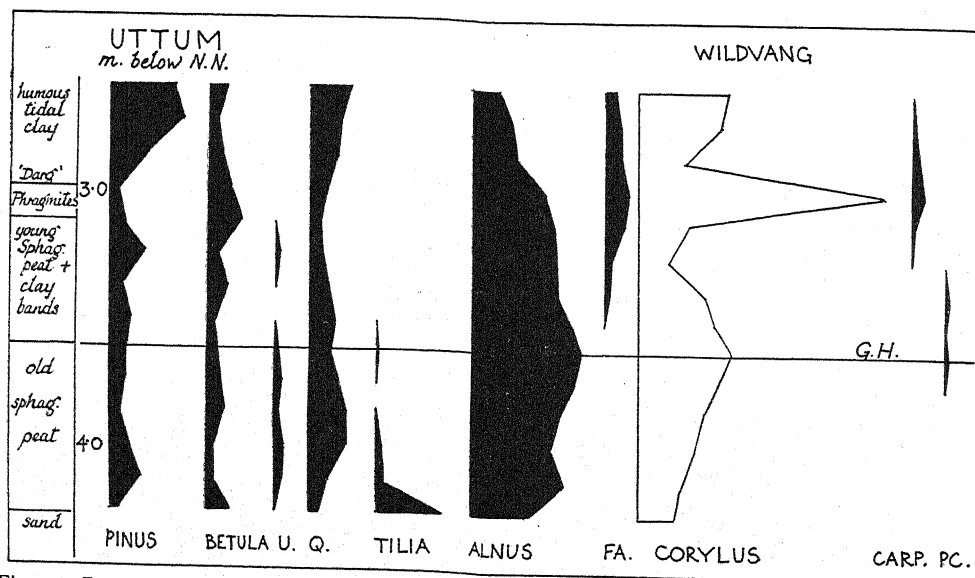
Fig. 19. Profile at Uttum, showing oligotrophic peats indicative of marine recession at the *G.H.* period, between the clay deposits of preceding and succeeding transgression.

The salient points disclosed by this evidence seem to be:

(1) The rapidity and great vertical extent of the transgression in zone VI (Schütte's Senkung I).

(2) The pronounced slowing off of this transgression in zone VII.

(3) An unmistakable marine retrogression in the period embracing the *G.H.* (Schütte's Hebung III).

(4) Resumed transgression during the first centuries A.D. (Schütte's Senkung IV).

It is further probable that standstill or minor retrogression interrupted transgression in the middle of zone VII, this constituting Schütte's Hebung II.

This is substantially the same history as that for Holland and for the East Anglian fenland, save that in the last-named area there is only a trivial amount of post-Roman transgression.

E. SCHLESWIG-HOLSTEIN AND DENMARK

The average marsh profile described by Ernst (1934) for the island of Föhr consists of:

Clay—averaging 2 m. in thickness, but sometimes up to 4 m.

Fen Wood peat—averaging 1·5 m. thick, but up to 2·3 m.; this bed rests upon various kinds of transition peat, and generally gives place upwards to mesotrophic, but not raised-bog peat.

Sand—rearranged glacial or post-glacial material.

The base of the peat now lies at not more than 5·0 m. below sea-level, and Overbeck has assumed that peat growth was dependent upon rising ground water, caused by slow marine transgression. There is no evidence of discontinuity between the peat and the overlying marine clay, and no proof of marine retrogression is present, although rise of sea-level must have been slow or absent when the peat was forming.

Dating of the peat and clay is somewhat helped by the discovery in the peat of polished and unpolished stone axes and of Neolithic pottery, whilst Iron Age graves seem to have been made within the period of clay deposition. The pollen diagrams do not give very decisive help, partly because of the local over-representation of alder in the peat. *Fagus*, however, shows occasional grains in the peat and a continuous curve through the clay of several profiles. By comparison with mainland diagrams, such as those from Kollund (Fig. 4), Ernst concludes that the peat formed from about 3500 to about 800 B.C., and that tidal clay was deposited from the latter date until the dyking of the fifteenth century. This estimate is interesting, as both Ernst and Overbeck point out, in that it indicates that tidal silt was forming here at a time when, on the German coast opposite, marine retrogression was taking place. This ought not to surprise us unduly, for there is good evidence from fine-levelling measurements that to-day, whilst northern Schleswig-Holstein is rising, the Oldenburg coast is sinking, and between is a belt of little perceptible change (Schütte, 1935). Although the movement is now opposite to what it formerly was, it is clear that tilting movements exist between the region of Föhr and the north-west German coast. It is apparent that as we here enter the area of predominant post-glacial isostatic land elevation, the absence of deep marsh deposits such as those of the Dollart coast and of Holland is only to be expected. We have therefore less opportunity of assessing any but the relatively recent phases of coastal history.

In Denmark we first encounter the clear manifestations of the isostatic land elevation caused by recovery after removal of the ice load which depressed the earth's crust during the last ice age. This elevation is recorded in the present altitude of considerable raised beaches and terraces, which occur north of a line from Bovbjerg to Gedser, and which have been collectively known as the *Tapes* beaches on the Atlantic coasts and as the *Littorina* beaches on the Baltic side. The melting of the great thickness of ice in the post-glacial climatic amelioration led also to a purely eustatic rise in sea-level of the order of 80 m. extent. The interplay of the eustatic and isostatic factors in marginal countries such as Denmark has produced very complex phenomena, but the intensive attack on this and

other problems of quaternary geology has been very helpfully supplemented by application of pollen analysis methods.

At the close of the late-glacial period, Jutland was continuous with southern Sweden, the Baltic an ice-dammed sea with an opening through the Öresund and the Great Belt. At the beginning of the post-glacial the Baltic was opened by recession of the ice, thus causing the cold salt-water stage known as the Yoldia Sea. Before long, elevation closed the Baltic once more, and it became the fresh-water *Ancylus* Sea, with an outlet at first through central Sweden, and later again through the Great Belt.

The 'continuous land period' (Fastlandstid) apparently extended from the late-glacial through to the later part of the *Ancylus* Sea stage of the Baltic. Submerged peat beds lend evidence upon this point. Thus pine stumps from Kåseberga in Schona (south Sweden) are related by Jessen to the same stage of forest history as the peats of the North Sea moorlog, i.e. our zones IV and V. Other deposits suggested by Jessen to be of the same age are beds with pine stumps from 40 m. below sea-level in the southern Baltic, north of Rügen, and also south-west of Bornholm. Nearer present sea-level we have peat submerged 13–15 m. deep in the Kongedyb off Copenhagen. The analysis of this peat by Jessen (1935a) is given in Table 4 (p. 46), and it may clearly be referred to the end of our zone V or the opening of zone VI. The same bed yielded macroscopic remains of alder, birch, dogwood, hazel and lime.

A very valuable observation is that also given by Jessen (1935a) on the pollen spectrum of the lowermost samples from the basin of Fil Sö, 30 km. north-west of Esbjerg (see Table 4). This sample came from 6 m. below sea-level, where it underlay brackish water deposits. Although this analysis gives 30% alder pollen and high values for the mixed-oak forest trees, pine and birch contribute together 43% of the total tree pollen, and it seems unlikely that the bed formed later than the opening of zone VII. It is interesting to note that in relation to this analysis Jessen makes the point: 'It seems as if the submergence of this North Sea continent was established rather quickly, for already towards the end of the Boreal period...brackish water deposits had penetrated into the basin of Fil Lake.'

It will be recognized that whilst the Baltic remained isolated from the North Sea, as the fresh-water *Ancylus* Sea, its level changes were independent of those of the world's oceans, but this condition ended with the opening of the Sound and the conversion of the Baltic into the *Littorina* Sea. This event is held, on the evidence here given, to have occurred at about the transition from zone VI to zone VII, that is, the Boreal-Atlantic transition. After this time the evidence of littoral deposits of coasts in the western Baltic may be drawn in to supplement our evidence of the North Sea's coastal history. There is no question, therefore, of the validity of the evidence now to be mentioned from the islands of Als and Sjaelland.

In 1935 Jessen (1935b) described the results of excavations at a filled-in fiord at Bundsø on the northern shore of the island of Als. The stratigraphy in the deepest boring showed a basal fresh-water lake mud, overlaid by brackish-water mud containing shells of *Cardium edule* and *Hydrobia ulvae* as well as a diagnostic diatom flora. The pollen analysis of the profile is given in the diagram of Fig. 4. From this it is apparent that the fresh-water fiord deposits were formed between our horizons *H.* and *B.A.T.*, and that invasion by salt water first took effect very close to the latter horizon. From their present level the fresh-water beds must have been formed when Als lay some 4·4 m. higher than at present,

so that by the opening of zone VII the marine transgression had reached within this distance of present sea-level. The uniformity of the brackish water fiord deposits indicates that the rising sea never attained levels above those already reached by the middle of zone VII, when Neolithic people lived on the shore and left traces of their occupation in the marginal deposits. The old view, however, of a single *Littorina* transgression, with its maximum about 4500 B.C., and contemporaneous with the Ertebølle culture (represented by numerous midden sites on the old shore line), has now given place to more exact concepts based on closer investigation. J. Iversen (1937) made combined use of pollen and diatom analyses in the sites at Søborg Sø and Klampenborg Fiord in Sjaelland and Korup Sø in Djursland. The siliceous diatom valves are identified, counted, and referred to their ecological category as indicators of fresh, brackish, or salt water, so that throughout a vertical series of fiord deposits former variations in salt content of the fiord water can be graphically expressed. Iversen's results show that during the course of what had seemed to be one marine transgression, salt water had four times reached maximal concentration in the fiords, though between whiles the water had become almost fresh again. Moreover, pollen analysis showed these variations in salt content to have fallen at the same time in the different fiords investigated. The detailed pollen diagrams permit a close correlation of the coastal history with the forest sequence. The 'Early Atlantic' marine transgression is shown to have occurred in the beginning of Jessen's Period VII (just above the *B.A.T.* horizon). The two following maxima, which are not always readily separable, are together referred to the 'Middle Atlantic' transgression, and these fall in the middle of Jessen's period VII. The 'Late Atlantic' transgression comes in just before the beginning of Jessen's period VIII, and continues during the early part of it. It should be noted that all the marine deposits of the fiords lie within a narrow vertical range (3 m. only at Korup Sø, 4 m. at Klampenborg, and 5 m. at Søborg Sø), so that it seems likely that only small differences in sea-level are here concerned.

Iversen's conclusions have now been supported by the work of other investigators. Jessen (1939) has reported on investigations at Tengslemark, on the north coast of Odsherred. Here a small lake-basin, Klintsø, is filled with fresh-water lake mud to a height of 2·5 m. above present sea-level. It is now separated from the sea by the highest beach ridge of the district, but layers of salt-water gyttja show it to have been twice in open connexion with the sea. The pollen diagram (Fig. 5) can easily be correlated with those of Iversen, and it is apparent that the sea entered the little lake in the middle and late Atlantic transgressions. The transition horizon between Jessen's periods VII and VIII corresponds to our *Ul.* horizon, and is well expressed at Klintsø, as in practically all eastern and northern Danish diagrams. Jessen gives considerable weight to its recognition, and reports that at Gammelung Bog in Langeland an occupation level of the Early Neolithic coincides closely with this horizon. This confirms the early Neolithic age of the late Atlantic transgression, and confirms our transfer of the *Ul.* horizon from Britain to Denmark.

Just as the *Littorina* transgression was formerly thought one event, so prehistoric settlements on the *Littorina* shore were referred to a single mesolithic (Ertebølle) culture, and as the transgression has been shown to have been multiple and of long duration, so the settlements have been shown to belong to various periods. The reinvestigations by Troels-Smith (1937) at Brabrandsø indicate this clearly. Pollen analyses show that here also salt water entered the lake during Jessen's zone VII, and the rising sea-level reached

its maximum at the transition from zone VII to zone VIII. Thus the lake deposits formed during the middle and late Atlantic transgressions. The Brabrand culture layer was shown to correspond with the transition horizon between pollen zones VII and VIII (Jessen) and hence to have a Neolithic date, although typologically part of the Ertebølle culture.

The results of these investigations suggest clearly that in Denmark as in Germany the rapid and extensive transgression of our zone VI had come within a few metres of its final maximum by the opening of zone VII. Thereafter transgression was slight, and though progressive, was interrupted by phases of minor retrogression or arrest. The last and highest of the *Littorina* transgressions fell at about the *Ul.* horizon.

Jessen makes effective use of the Danish results in comparison with those of the German Baltic coast, pointing with especial emphasis to the consequences of Wasmund's analyses of submerged peat at Heiligenhafen, 50 km. east of Kiel. This peat is overlain by marine mud at a depth of 13–14 m. below present sea-level, and the top of it is referred to 'the end of the first half of the oak-forest period'. Since this clearly shows the Baltic transgressing a level of $-4\cdot4$ m. at Bundsø far earlier than it reached a level of -13 m. at Heiligenhafen, Jessen concludes that inhomogeneous movements of the earth's crust (ungleichförmige Schollenbewegungen) must have been responsible. Various subsidiary points of evidence given by Jessen to support this point of view need not be repeated here.

F.   SOUTH SWEDEN

The progress of recent investigation of sea-level change in southern Sweden has shown the situation to be of great complexity, so that we propose to restrict our consideration to the chief data presented by two workers most concerned to correlate forest history and sea-level changes in this region, L. von Post and T. Nilsson. Nilsson's detailed and convincing elaboration of the Scanian pollen-diagram type gives a very trustworthy reference scheme, by which we can fix the stages of sea-level movement in appropriate coastal sites. Three such sites on the Swedish west coast are Änggården in Göteborg (Sandegren, 1923; von Post, 1928), Lunna Mosse in north Halland (Halden, 1922; von Post, 1928), and Höganäs (von Post, 1928; Halden, 1929; Rydbeck & von Post, 1929).

At Änggården marine sand and mud rest upon a forest soil which is at 16·0 m. above present sea-level, and which is therefore 9·5 m. below the maximum of the post-glacial land submergence. Sandegren's pollen diagram through these deposits shows the peaty soil to have formed about the time of the *H.* horizon. The transgression of this bed and deposition of sand and sea clay upon it followed at a time somewhat before, and also after the *B.A.T.* horizon. It appears from this that the sea rose some 10 m. after the peat formation, but that the rise after our *B.A.T.* horizon was considerably less.

Somewhat farther south along the Swedish coast at Lunna Bog is a site for which Halden has given both diatom and pollen diagrams. Here fresh-water mud is overlaid in turn by fern (*Thelypteris*) peat, *Cardium* mud, diatom mud, drift mud, and peat. Diatom analyses show the maximum saltness to have obtained in the middle of the diatom mud formation. The pollen analyses, roughly speaking, indicate that the *H.* horizon lies at the base of the fresh-water mud; both this and the fern peat formed in our zones V and VI. Marine transgression took effect here at the end of zone VI, for the *B.A.T.* horizon lies in the *Cardium* mud. It is not easy to be certain, with the widely spaced analyses, but it seems likely that the *Ul.* horizon approximately coincides with the zone

of maximum saltness. The fern peat at Lunna Bog now lies at 9·5 m. above sea-level, with the level of maximum submergence some 10·0 m. higher, thus again indicating a submergence after the *B.A.T.* horizon, but of less extent than 10·0 m.

At Höganäs, Rydbeck, Halden and von Post co-operated in most fruitful investigations at a site where decorated deer-antler axes were found in littoral deposits close to present sea-level (Fig. 20). The stratigraphy of the most important exposure is given below:

Sea-level of Tapes beach in this region = 10·5 m. (in relation to present sea-level)
Ground surface level   = 3·8 m. (in relation to present sea-level)

m.	
2·0	Sand
1·0	Clay gyttja and sand
0·3	Muddy sand
0·95	Sandy gyttja with shells
(Contact horizon)	= − 0·5 m. (in relation to present sea-level)
0·25	Forest soil (wood peat)
1·0	Sand
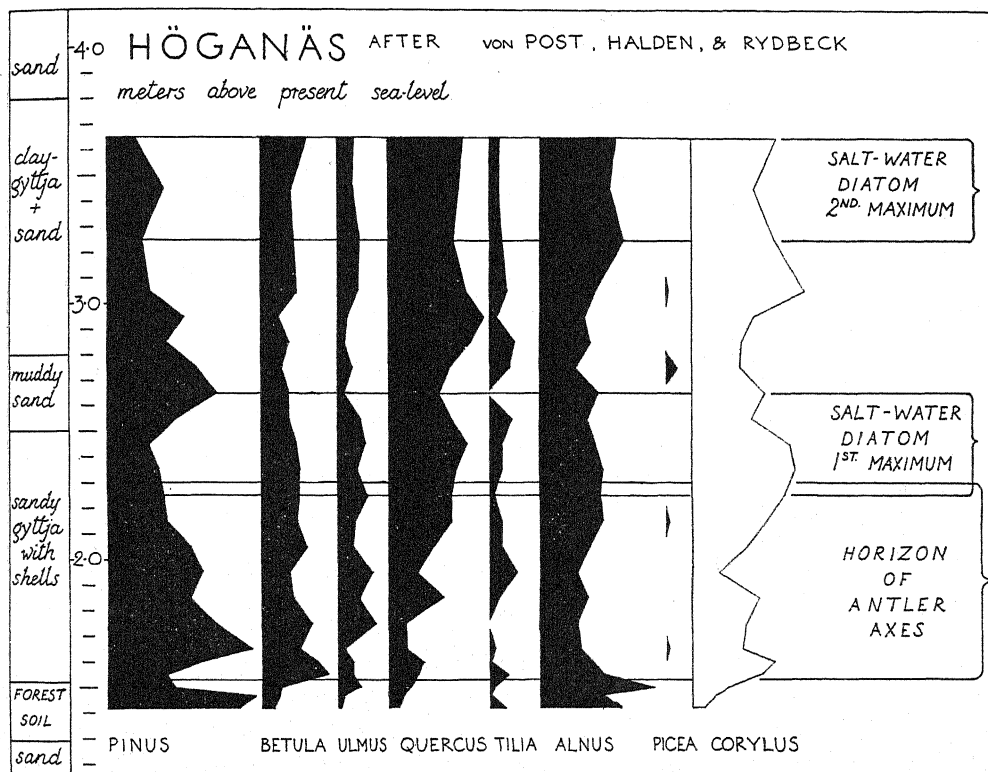
Fig. 20. Profile at Höganäs, south Sweden, showing correlation of stratigraphy, pollen-analysis, diatom analysis, and archaeology. The forest soil, now close to sea-level, was covered by the deposits of the maximum *Littorina* transgression.

By diatom analyses Halden demonstrated two clear transgression maxima in the gyttja layers above the peaty bed, and von Post made a detailed pollen diagram right through the profile, which Nilsson has later fitted to his own Scanian series. Nilsson concludes that the marine contact falls in his zone VI*a*, which is just above our *B.A.T.* horizon. He places the first transgression maximum in his zone V, and the second, near the top of the marine mud, close to the end of his zone V, that is to say, just before our *Ul.*

horizon. There is no reason to question these zone references, and we can therefore recognize that between the *B.A.T.* and *Ul.* horizons a net transgression of 10·0 or 11·0 m. occurred.

By investigations at several other sites on the south Swedish coast, Nilsson supports the view that over this region as a whole the transgression contact of the rising *Littorina* Sea falls close to the boundary between his zones V and VI, that is, just above our *B.A.T.* horizon. From this evidence, and by reference to Jessen's analyses from Kongedyb in the harbour at Copenhagen (see Table 4), he fixes the opening of the Baltic to the North Sea at the boundary between his zones VI and VII, which is our *B.A.T.* horizon. At this time sea-level reached the Darss Sill, which now is 18·0 m. below the sea surface.

After reviewing the growing weight of evidence that the *Littorina* transgression in Scania was multiple in character, Nilsson concludes that the absolute maximum was reached in the latter part of his period IV, within the Neolithic period. This is definitely later than the *Ul.* horizon as shown in Scanian diagrams, whereas in Denmark and Britain it seems that the *Ul.* horizon and the Neolithic period coincide fairly closely.

It seems probable that there was no large regression intercalated in the period of the *Littorina* transgression between *B.A.T.* and the Neolithic period, nor after the latter up to the present day are any substantial changes of land- and sea-level recorded on the Scanian coasts.

Although the picture thus derived of the course of the *Littorina* transgression in southern Sweden is so coherent, it must not be overlooked that it is over-simplified. South of Kåseberga, in some 35 m. of water, there have been found pine stumps and a peat layer, the pollen analysis of which, by Isberg, is to be seen in Table 4. Both von Post and Nilsson recognize the relatively late age of this peat, Nilsson putting it in his zone VII, and both he and von Post agreeing that it appears to imply considerable regression in the southern Baltic between the *Ancylus* maximum and the opening of the *Littorina* Sea. One is naturally reminded by it of the 'inhomogeneous earth crust movements' invoked by Jessen for the same region (see p. 58). Other recoveries of pine stubs from the south Baltic, such as those from 80 m. depth, northwards off Bornholm, might well be related to the same episode, although other peat samples with remains of pine from a depth of 59 m. at other south Baltic sites seem, from their pollen analyses, to have formed at a much earlier time.

G. FRANCE AND BELGIUM

In attempting to bring within range of this review the deposits of the coasts of France and Belgium, we recognize both favourable and adverse aspects of the task. It is unfortunately true that very few analyses have been made in coastal peat-beds in this region, nor, for such as there are, is there any developed network of pollen-analysis sites in the hinterland, from which a background scale of forest history can be established. On the other hand, as late as 1924 Dubois published a most comprehensive and valuable memoir on the geology of the quaternary deposits of the coast of northern France, and the value of this for our purpose is much greater because the author not only devoted a large part of the memoir to the post-glacial deposits, but brought them into relation with the geological history of southern Scandinavia.

Dubois employs the term 'Flandrian' for the last great period of marine transgression on the Flamand coast, a transgression associated primarily with the melting of the great

ice-sheets after the Würm glaciation. He divides the transgression into three stages, as follows (see also Fig. 21):

(1) *Assise d'Ostende:* beds 26–33 m. deep, with a mixed Boreal and Atlantic fauna, together with a few arctic forms. *Corbicula fluminalis* occurs in the basal beds.

(2) *Assise de Calais:* beds 15–20 m. deep, with a restricted marine fauna typical of the upper littoral belt.

(3) *Assise de Dunkerque:* fauna of to-day in *Cardium* sands and *Scrobicularia* clays: these deposits were formed at times known historically to fall within (*a*) third to eighth century A.D., and (*b*) thirteenth century A.D.

These divisions were based largely by Dubois upon the faunal content, and this is effectively employed to achieve correlation with northern Europe. Thus *Corbicula fluminalis* is the characteristic early post-glacial form, and *Mya arenaria* the latest. Between the first two transgressive stages are beds of mud and peat at altitudes of about −15 and −20 m., corresponding to a stage of arrest or slight retrogression. These occur at Ostend, Coquelles, and Calais, and Dubois has no hesitation in correlating them with the *Ancylus* stage of the Baltic. This directly suggests reference to our pollen zone VI. In relation to this we should consider the result published by Lemée (1938) of pollen examination of a peat bed underneath alluvium and at 13 m. below sea-level, in the valley of the River Orne at Bénouville. Here the pollen of pine was preponderant (some of it large, and presumed to be that of *Pinus montana*), though there were rare grains of birch. Lemée, who claims to have recognized in Normandy a series of forest phases analogous with those of north-west Germany, the Netherlands and England, places this sample in the period before extension of hazel and the mixed-oak forest. It seems probable that the sample in question corresponds, as Lemée says, to the earliest stage of the Flandrian transgression, the period of formation of the Dogger Bank peat. This occurred in our zones IV and V, and peat formation at a site now 13 m. below sea-level must have been quite possible then: peats of similar age were encountered 4 m. below sea-level in the King George V Dock at Southampton, England (H. & M. E. Godwin, 1940).

Occasional samples from between present tide-marks have also been subjected to pollen analysis by G. & C. Dubois (1935), but beyond the indication that they belong to the alder, mixed-oak forest stage of forest history, give us no more precise information. The deficiency is to some extent made good by the rather numerous archaeological discoveries recorded from the coastal peat beds, and of these Dubois has taken account in his memoir, among them the well-known submerged megalithic remains at Er-Lanic in Brittany (de Closmadeuc, 1882).

At Moulin de Luc, Calvados, a littoral peaty deposit has yielded both archaeological and pollen-analysis data. At this site Hue (1938) has described a bed of peaty calcareous marsh clay, 75 cm. in thickness, overlying sand. The peaty layer contained abundant wood and artefacts, among the latter being a 'Neolithic' flint industry, and abundant Gallo-Roman pottery. The level on the shore is not given, nor is it evident whether the bed constituted a living surface for a very long period, or was twice occupied.

The pollen analyses by G. & C. Dubois (1938) are from five samples, but based unfortunately upon very small counts. Two samples contain much alder and beech, together with mixed-oak forest pollen: two other samples have only alder and beech with hazel. Thus the beds are certainly later than our zone VI, and might come as late as zone VIII, just as the archaeological remains suggest.

The investigations of Welsch (1917) show that submerged peats occur on the west coast of France as far south as Biarritz, and although these are not demonstrated to lie

NORTH·FRENCH COASTAL HISTORY (after Dubois)				
	Stages	Sea-level	marine beds	land deposits (& correlations)
FLANDRIAN UPPER	Assise de Dunkerque (O)	present level	marine deposits of 13th century.	
				Mediaeval land-surface
	Mya immigrates	transgression	marine deposits 3rd to 8th centy.	
				Gallo-roman land-surface
FLANDRIAN MIDDLE	Assise de Calais (O to –15 m)	stillstand or regression		Peat with Neolithic & old metal age
	no Mya arenaria	transgression	Beach. marsh-clay grey-blue sand	(Dosinia) (old Tapes)
FLANDRIAN LOWER	Assise d'Ostende (–15 to –30 m)	stillstand or regression		Peat (Ancylus)
	many species disappearing e.g. Corbicula fluminalis	transgression	Corbicula sand + Estuary clay.	
				peat of Dogger Bank.
MONASTIRIAN				

Fig. 21. Scheme of north French coastal history according to Dubois (1924).

under sea-level, they are now between tide-marks, and being of considerable thickness, almost certainly reflect some submergence, presumably the result of eustatic rise in sea-level. Pollen analysis of these beds has hitherto been sparse and not very illuminating.

Since the analyses mentioned here represent substantially all the pollen-analytic evidence, it is clear that they do no more than lightly reinforce Dubois' schema. This latter readily falls into accord with the data already discussed, although it is hard to see why Dubois sets a limit of 30 m. to the amplitude of the Flandrian transgression as a whole.

H. CONCLUSIONS

The evidence discussed in the foregoing pages has been summarized in Fig. 22, from which certain broad consistencies of behaviour are apparent: these are considered in turn below.

(i) *Great eustatic rise in zone VI*

It is perhaps the most outstanding result of this survey that one can record everywhere from the west continental coast, that very rapid transgression was in progress during zone VI, and by the end of this time sea-levels within a few metres of the present ones had been reached in all those regions not suspected of complicating isostatic effects. Everywhere the *B.A.T.* horizon, which terminates zone VI, is more or less closely associated with transgression contacts not far from present sea-level, and it was during zones V and VI that the North Sea, in all probability, gained the greater part of its present extent.

In the succeeding zone VII the diminishing rate of eustatic rise in ocean level permitted the expression of considerable local differences in transgressive and regressive effects.

(ii) *Culmination of eustatic rise in zone VII* (Littorina *period*)

In zones V and VI there was very rapid and extensive eustatic rise in sea-level, during which the oceans came within a few metres of their present height.

In zone VII there were a few metres more of slow eustatic rise, which in regions of isostatic uplift kept pace with such uplift, and allowed the formation of beaches subsequently raised by continued isostasy above sea-level. These are the complex of *Littorina* beaches, and the time of their formation the so-called 'Littorina' or 'Atlantic' period. It is evident that this period is one of *culminating* eustatic transgression, just as the preceding period (embracing the so-called 'Boreal' or '*Ancylus*' periods) was one of *rapid and extensive* eustatic transgression. The concept ought to be abandoned that it was the Atlantic period which, more than others, was characterized by marine transgression: it merely produced evidence of the final, or almost final, stages of such transgression.

It is evident that what we know of climatic history speaks strongly in favour of the view we advance. Since the major post-glacial eustatic change in sea-level can with certainty be attributed to water contributed to the oceans by the melting of the great ice sheets, we can postulate when it is that we ought to expect the greatest rate and most extensive progress of eustatic rise in sea-level. It is natural to suppose that this took place under those conditions of rising temperature which alike caused the sudden replacement of birch and pine forests by mixed-oak woodland with alder and hazel, and the introduction of warm faunas into our tidal waters. These conditions obtained in our zones V and VI, when temperatures became high and supplies of melting ice were yet large. After zone VI, though temperatures remained high, the mass of ice liable to melting had become small, and though high *maximal* values for eustatic transgression might be reached in zone VII, the great period of restoration of water to the world's oceans should surely be expected to have ended before this.

	S. Sweden	Denmark	Föhr	N.W. Germany	Holland	Flamand coast	Britain East & South	Britain South-west
Pt					submergence?		submergence	submergence
VIII (ROMAN IRON-AGE G.H)	emergence	little movement	submergence (marsh-clay)	submergence	submergence R.K.=-3m.	submergence (Dunkirk beds)	emergence (wood peat) &c.	emergence (raised-bogs)
VIIb (BRONZE AGE)			emergence	emergence (raised bogs)	emergence (raised-bog)	emergence	submergence (fen-clay)	emergence
ul (NEOLITHIC)				? slight emergence	T.K.=-5m.			
VIIa (MESOLITHIC)	submergence	submergence	submergence	submergence	submergence (old sea-clay)	submergence (Calais beds)	submergence	emergence
B.A.T.	T.K.=0 upwards	T.K.=-6m.		T.K.=-17m.	T.K.=-12 to -24		T.K.=>-7m.	T.K.=+1
VI / V	submergence	submergence	submergence	submergence	submergence	submergence (Ostend beds)	submergence	submergence
H / IV		(DEEP	MOOR	LOG	-35 m.)			

T.K. = Transgression contact.
R.K. = Regression contact.

Fig. 22.　Co-ordination diagram of results, showing land- and sea-level relations at different stages of forest history, expressed by the zones and horizons for England and Wales. (Stages of marine regression are indicated by shading.)

(iii) *Eustatic fall in sea-level at close of zone VII, and early in zone VIII*

In south-west Britain, the East Anglian Fenlands, northern France, north-west Germany, and Schleswig-Holstein, there is strong evidence of emergence in the period at the close of zone VII and opening of zone VIII: it decisively embraces the time of the *Grenzhorizont* and of the preceding Bronze Age: it is less certain if it extends so far back as the Neolithic Age, and how generally it extended towards the Iron Age.

The widespread extent of the emergence into regions far from the centres of isostatic recovery, and at a time so long distant from the major diminution of the ice load, strongly suggest that we have here evidence for a eustatic fall of sea-level of some magnitude. In the data we have been considering there is little exact information as to the magnitude of this fall, but to have permitted the establishment and growth of big raised-bogs over marine and semi-marine beds, some 3–5 m. at least must have been involved.

If we accept the fact of this eustatic effect, a curious consequence is seen to follow: although northwards from Germany we should expect the emergence to be still more pronounced as isostatic uplift reinforced the eustatic effect, in fact in Schleswig the emergence had given place to submergence by the Iron Age, and in Denmark there seems no clear evidence of emergence after the *Ul.* horizon. These facts can only mean that in the region of Denmark and Schleswig there was a belt of isostatic depression during this period.

(iv) *Eustatic rise in sea-level in zone VIII*

There seems reason to suppose that a small eustatic rise in sea-level occurred not long after the opening of zone VIII, although it is archaeological, rather than pollen-analytic, evidence that provides the dating. Already in Britain evidence from Somerset, Wales, and East Anglia has been given to support the view that in Romano-British, and perhaps also in Iron Age times, marine transgression was in progress. Evidence for a eustatic rise in sea-level at this time has also been reported by von Post from Sweden, and by Hyppa from Finland. To this we may now add the evidence of Iron Age submergence in Föhr. In north-west Germany, Holland and France it is clear that transgression was taking place in immediately post-Roman times, and it is uncertain how much earlier than this the movement had begun.

(v) *Differential movements since the B.A.T. horizon*

In the course of this paper, and of the preceding one on the coastal peats of the British Isles (1943), we have mentioned several instances in which deductions may be made of the relation of present sea-level to that at the time of the *B.A.T.* horizon. These data are collected in Fig. 23, from which it will be seen how the land has moved in relation to sea-level during the period concerned. It is evident that the isostatic recovery of Scandinavia, Scotland, and northern Ireland is represented by the positive figures in those regions. Figures in Wales, Somerset, and at Höganäs show very little net movement, but in north Germany and Holland there has been a big net subsidence, to which the values in Denmark are certainly transitional, and those in East Anglia probably so.

Some very interesting conclusions appear to follow from consideration of these figures. It seems that in order to bring the Dutch and German transgression contacts to their present levels *either* the eustatic rise between the *B.A.T.* horizon and to-day was of the order of 20 m., *or* there was a large basin of depression formed in the time in question,

affecting Holland and Germany to a large extent, and East Anglia to a less degree. In regard to the first view it should be noted that if the *Littorina* beaches of Scandinavia have indeed been produced by eustatic rise keeping pace for some time with isostatic uplift, then the net rise of 10 m. in sea-level between the *B.A.T.* horizon and the *Littorina* shore at Höganäs must be a minimal figure for the eustatic rise. In support of the second view we may note that the pollen-analytic evidence has been used to demonstrate that tilting must have occurred in the given period between the west and east of Britain, and we may also recall Jessen's assumption of inhomogeneous earth crust movements between Denmark and Kiel already mentioned.
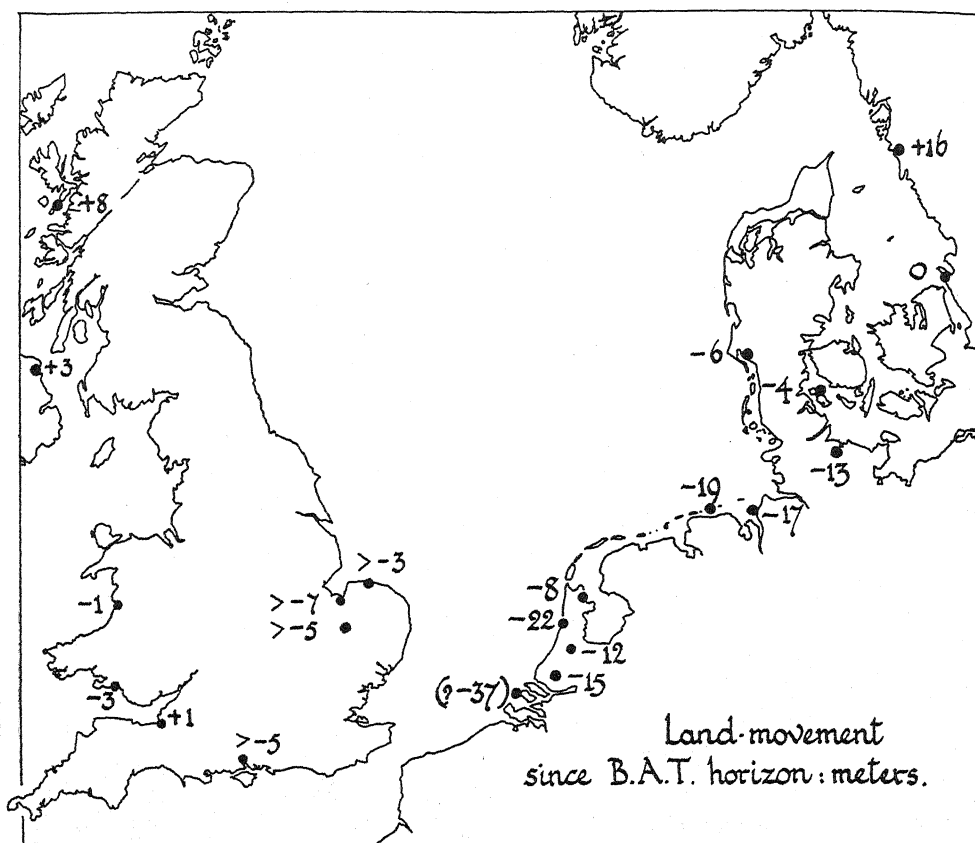
Fig. 23. Map of the North Sea region to show net movement of land in relation to sea-level between the *B.A.T.* horizon and the present day.

The high levels for the *B.A.T.* transgression contact in Somerset and in Wales lead to the conclusion that either (i) submergence continued later in zone VII in Denmark and southern Sweden than it did here, or (ii) the forest zones were later in spreading in Somerset and Wales than in Denmark. Against the latter view is the fact that the climate was at this time becoming more atlantic in character, and Somerset and Wales are more, and not less, atlantic than Denmark, so that as far as forest expansion was climatically determined, it should have been earlier in the west of Britain. This applies with especial force to the expansion of *Alnus*, if increasing wetness is considered responsible for its sudden expansion at the opening of zone VII.

If the former view is correct, then the facts must be viewed in relation to a conception of the Scandinavian *Littorina* transgression as a eustatic rise in sea-level, overtaking for the time being the progressive isostatic recovery of that region after depression during the ice age. In this case in Somerset and south Wales, which lie still farther outside the centre of isostatic recovery, the same eustatic rise should have given at least an equal transgression, and one later, or at least equally late, in reaching its maximum. Now in Somerset after the end of zone VI it seems certain that there was no substantial transgression until the Romano-British period. Something like this is true also of Borth, although in Swansea Bay a small amount of transgression is evident.

It follows that during this time either southern Scandinavia sank isostatically or Somerset and south Wales rose isostatically, or possibly both. The first hypothesis seems unattractive in view of the conclusions of Swedish quaternary geologists, but the second involves Somerset and south Wales in rates of isostatic rise of considerable magnitude, and in any case larger than those in south Sweden at the same time. The problems thus raised evidently demand much more investigation.

The survey we have now made has been a preliminary essay only. Despite omissions and deficiencies of treatment it indicates how useful may be the application of pollen analysis to problems of quaternary land- and sea-level change. It ought, moreover, to serve to direct attention to the most outstanding difficulties of the problem, to indicate in what fields of it the attack can be most profitably renewed, and to show what kinds of evidence must be sought when circumstances again give opportunity for the extensive field and laboratory investigations which will be needed.

Summary

By a restricted series of pollen diagrams from the lowland coastal region of the North Sea, it has been shown that the major horizons recognized in the pollen zonation for England and Wales can usefully be extended over the whole area. By the use of these horizons applied to pollen analyses of submerged peats and alternating fresh-water and marine deposits in suitable places, a co-ordination has been made between coastal beds in France, Belgium, Holland, north-west Germany, Denmark and south Sweden.

From this it appears that during zone VI, the period of rapid climatic amelioration, when mixed-oak forest first extended in western Europe, there was a rapid and very extensive eustatic marine transgression affecting the shores of all countries bordering the North Sea. We do not know how far this rise in sea-level was operative in the preceding zone V. In the succeeding zone VII, however, the eustatic rise culminated, but reached its final values at a much slower rate and with only a few metres further rise. It seems desirable on this account to abandon the concept of this period (the Atlantic period) as one *par excellence* of extensive marine transgression, and to regard it only as the time of culmination of such transgression.

At the transition between zones VII and VIII, a period extending over parts of the Bronze and Iron Ages, and including the *Grenzhorizont*, there was a eustatic fall in sea-level. A further eustatic rise probably took place in Romano-British times.

The effects of isostatic recovery from ice-loading are taken account of in Scandinavia, but in addition the evidence seems to show other differential tilting movements of the

earth's crust, there being indications of a region of isostatic depression over Denmark and Schleswig-Holstein in the Bronze and Iron Ages, and over north-west Germany, Holland, and perhaps East Anglia, between the *B.A.T.* horizon (Boreal-Atlantic transition) and the present day.

It is a great pleasure to acknowledge the constant help in translation of Scandinavian papers given to me by Mr H. Gilbert-Carter, Director of the Cambridge Botanic Garden.

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FURTHER EXPERIMENTS ON TORSIONS OF LEAVES

By R. SNOW

Fellow of Magdalen College, Oxford

(With 10 figures in the text)

1. Introduction

In a previous paper (1942) experiments were reported which were made in order to determine in which direction leaves placed on edge would twist in response to the stimuli of gravity and overhead light, if they were cut off at the base and fixed distally. It was there explained how it is that the answer to this question can decide between the two main kinds of theory of the mechanism of active torsion, the oblique elongation theory, or, better, helical theory of Schwendener & Krabbe (1892), and the transverse growth theory of Rawitscher (1932), and the distinction between these theories will be further considered at the end of the present paper. The results obtained were that the rachises of certain pinnate leaves fixed distally twisted in the 'normal' direction—i.e. so as to bring their morphologically upper surfaces towards the top—in accordance with the transverse growth theory, but the pulvini of *Phaseolus* and *Wistaria* twisted in the 'abnormal' direction in accordance with the other theory. But these torsions of detached leaves were not very big, though consistent in direction, and later when the same method was applied to the petioles of various simple leaves, it was not found very satisfactory. So it became desirable to find a new method of setting leaves free at the base, which would enable them to respond more strongly, and the results of experiments with such a method will be reported here. Experiments will also be reported on the effects of stimulating constrained petioles and pulvini, and on torsions of petioles to which auxin was applied locally.

In the previous paper (1942, p. 4) it was written: 'Rawitscher (1932, p. 203) states, without giving details, that an organ fixed at the tip twists the opposite way to the normal, although if it does so this is inconsistent with his own hypothesis.' But Prof. Rawitscher has since informed the writer that the sentence in German is ambiguous, and may have meant either this or else that an organ fixed at the tip twists into a helix of the opposite sense, which would agree with his hypothesis.

2. The new method and a change of terms

The new method of setting leaves free to twist at the base was to cut away the tissues of a short zone of the base of the petiole, about 0·75 cm. long, until there remained in pinnate leaves only a narrow strip of the ventral part of the ring of bundles, or in simple leaves only the median bundle, together with a little surrounding parenchyma. Before this was done the leaves were fixed distally by placing a collar of plasticine round a distal zone of the petiole or rachis, or wherever it was needed, and tying the collar tightly between two narrow sticks (see Fig. 1). The conducting tissue which remained in the cut zone at the base was enough to enable the leaf to go on growing quite well, but yet

this narrow zone was quite limp and did not appreciably resist or transmit any torsional force, as was often verified with the fingers after the experiments. Instead it could be just twisted round like a thread. The cut zone was vaselined, and the plants, which were in pots, were kept fairly damp under bell-jars and screened partly or completely from direct sunlight, so that the light came mainly from overhead as before.

With the new method when the plants were placed horizontal so that the leaves operated upon were on edge, their petioles in some species started to twist in the direction which was previously called normal, and then continued to twist through more than 90°, so that they went beyond the normal position. So it will no longer be appropriate to call this direction of twist normal, and instead it will be called positive, and defined as that direction of twist which *at the start* tends to bring the organ into the correct orientation by the shorter way round. Some lateral organs, however, with which the present paper does not deal, are negatively photostrophic in the sense that they normally face away from the light. In these the normal torsions could, if necessary, be called negative.

3. THE RACHISES OF PINNATE LEAVES

Plants of *Spiraea arborea* were used which had been taken as cuttings from the same bushes as were used in the previous experiments (1942), though previously these were thought to be *S. Aitchisoni*. In each plant a young leaf of about half the final length had a zone near the base of the petiole reduced to a narrow strip and was fixed at a zone about two-thirds of the way up the rachis in the way described already. The pots were then placed horizontal so that the leaves were on edge. Since the rachises of these leaves were thin and weak, and were also curved by epinasty, they were supported after the operations on threads stretched horizontally below them.

In three leaves so treated the parts of the leaf-stalk between the distal fixed zone and the basal cut zone rotated by torsion through 90° in the positive direction, so that they regained the normal orientation. The torsions were completed in the three plants in 26 hr., 2 and 4 days, and were already conspicuous after 1, 1 and 2 days. The part of the rachis beyond the fixed zone also twisted itself into the correct orientation. So these torsions were in the same direction as those obtained previously with detached pinnate leaves, and they were more satisfactory in that they reached the full 90°. They support the transverse growth theory of torsion.

4. THE PULVINI OF *PHASEOLUS*

The distal pulvini of *Phaseolus multiflorus* just below the blades respond best and most rapidly. The petioles also respond well while young and growing, but a little more slowly, and the basal pulvini respond more slowly still.

The distal pulvini were tested by the new method in six seedlings in which the two primary leaves had reached about half their final length. In one leaf of each pair a zone at the base of the petiole just above the basal pulvinus was reduced to a narrow ventral conducting strip in the way described, and a zone at the extreme base of the blade, just above the distal pulvinus, was fixed in plasticine between sticks, as is shown in Fig. 1. To fix this zone without unduly distorting the blade beyond was a little awkward, but could be managed in leaves that were strongly cordate. The main veins gave enough
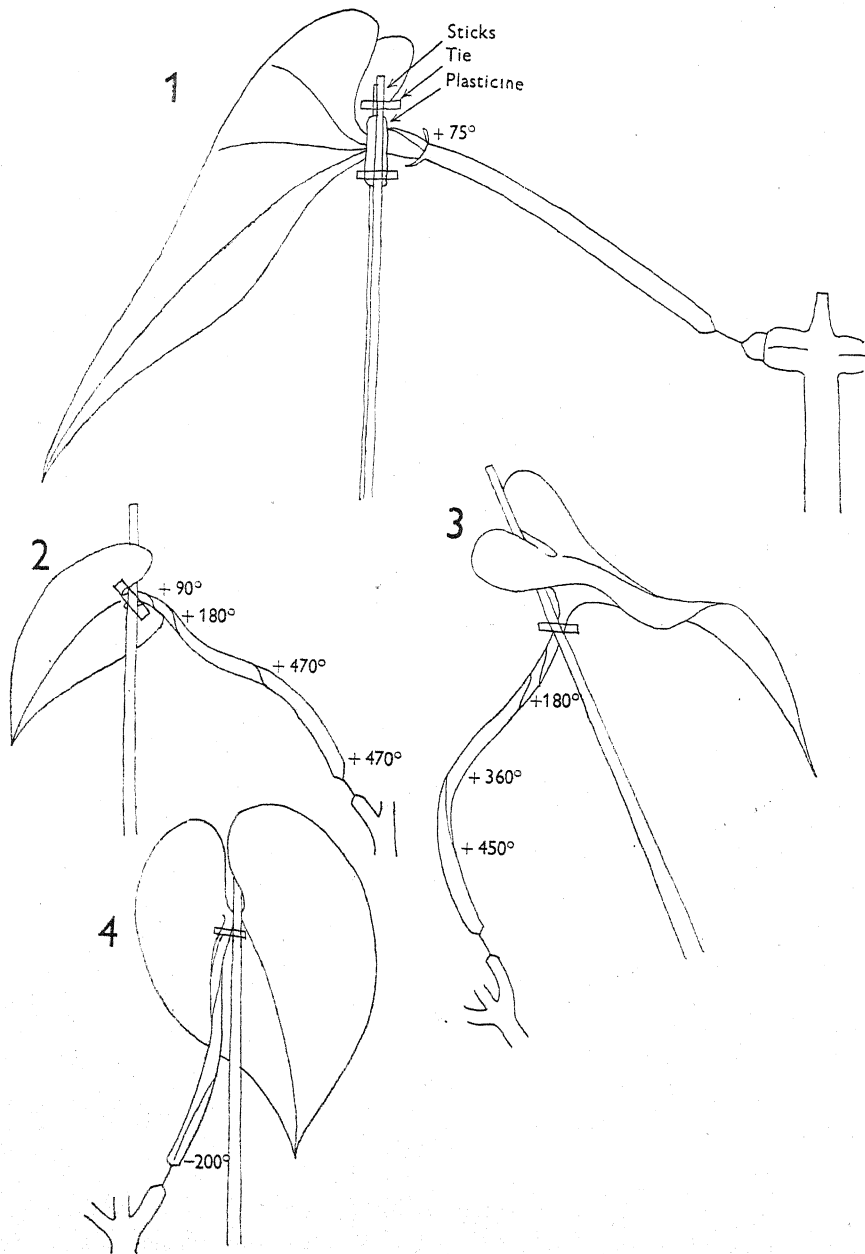
Figs. 1–4. Showing torsions in a pulvinus and in petioles of leaves fixed distally and arranged on edge. The leaves are drawn as seen from above. In Figs. 2–4 the plasticine collar and one of the two sticks are omitted. Fig. 1. *Phaseolus multiflorus* twisted +75° in pulvinus. Fig. 2. *Viola odorata* twisted +470°. Fig. 3. *Lunaria biennis* twisted +450°. Fig. 4. *Lunaria biennis* twisted −200°.

rigidity to the fixed zone. The pots were then placed horizontal with the leaves on edge as usual.

The result was a surprise: for in all six leaves the distal pulvini twisted positively, whereas previously those of the detached *Phaseolus* leaves had twisted negatively. Table 1 shows how the torsions developed in those four pulvini which responded best. It can be seen that in leaves 1 and 2 of the table the distal pulvini continued to twist for several days after the pulvini had reached the normal orientation, and that they finally twisted through 200 and 150°—very sharp torsions for such short and thick organs.

The petioles of these two leaves were of course carried round passively by the torsions of the pulvini, but in addition they themselves made positive torsions which started after 2 and 4 days respectively and reached maxima of 150 and 130° after 8 and 7 days. All these torsions beyond the normal orientation were presumably due to a directive influence which was transmitted continually from the stimulated blade, and was stronger than the effect of the stimulus perceived locally in pulvinus and petiole. For the blade beyond the fixed zone lacked the power to twist itself into the normal orientation, though it sometimes twisted a little.

Table 1. *Torsions in degrees of pulvini of leaves of* Phaseolus *fixed distally*

Leaf	1 day	2 days	3 days	4 days	5 days	8 days	11 days
1	0	+40	+60	+90	+100	+170	+200
2	0	0	+15	+60	+ 90	+150	—
3	0	+65	+75	+80	—	—	—
4	0	0	+20	+75	+ 80	—	—

Leaves 3 and 4 were not further stimulated after their pulvini had twisted through 80°, but instead the pots were placed upright again, whereupon the torsions soon diminished. In the remaining two leaves the torsions were feeble, but still clearly positive.

In view of these positive torsions, it seemed desirable to repeat the earlier experiments with detached *Phaseolus* leaves. So nine primary *Phaseolus* leaves, not quite fully grown, were cut off at the base, placed with their blades on edge, and fixed distally to supports by means of collars of plasticine placed round the base of the blades as before. Some were submerged under water and some were placed in practically saturated air and allowed to take up water through the marginal parts of the lower halves of the blades, which were kept just submerged and had the ends of some of their veins cut.

The distal pulvini twisted −30, −25, −20, −15, −12, −8, 0, 0 and +12°. The negative torsions all developed in the first 24 hr. and then remained constant, as also did most of those reported previously. But the one positive torsion of 12° did not start until the second 24 hr., and had nearly disappeared by the end of that period. So it seems to have been exceptional and of some different kind, and the results essentially confirm those reported previously and show that the pulvini of detached *Phaseolus* leaves fixed distally twist negatively.

It is perhaps significant that the positive torsions reported in Table 1 also did not start until the second day or even the third day, although they finally became much greater than those of the detached leaves. For this suggests that the positive and negative torsions are different in kind. But what is at present so puzzling is that it was only the pulvini of the leaves fixed distally which responded in opposite senses according to

conditions. The pulvini of *Phaseolus* leaves fixed by the base always responded positively only, alike whether the leaves were detached or attached normally to the stem.

For comparison it may be mentioned that the pulvini of similar *Phaseolus* leaves attached normally and stimulated in similar conditions were regularly clearly twisted after a few hours and sometimes after only 1 hr.

It now seemed of interest to determine in which sense the pulvini would respond if the leaves were attached to the stem by a strand of dead tissue only. For then they would be mechanically attached, but physiologically detached except for the effects of any substances travelling in the transpiration stream. So in each of four seedlings a primary leaf at about the usual stage was treated like those of Table 1 except that the zone at the base of the petiole was killed with a hot glass rod instead of being reduced to a strip by cutting. The dead zone quickly shrunk and became quite limp and without resistance.

Unfortunately, the pulvini did not respond well after this operation. In two leaves they did not twist at all, but in the other two they were found when examined after some days to have twisted −20 and −8°.

So it seems that what is needed for positive torsions in these pulvini fixed distally is a connexion through living tissue with the rest of the plant, and presumably such a connexion acts somehow on the physiological condition of the leaf. But the point needs to be tested further.

Since the positive torsions of the pulvini fixed distally and connected through living tissues were so strong, it seems probable that it is these which correspond the more closely to the responses of the pulvini of normal intact leaves, in spite of their delayed starts: and these torsions agree with the transverse growth theory.

5. PETIOLES OF SIMPLE LEAVES

The petioles tested with the new method were of the species *Viola odorata*, *Althaea rosea*, *Lunaria biennis* and *Stachys silvatica*, besides those of *Phaseolus* mentioned already. The plants were all young seedlings, except the violets and a few of the *Stachys*, which were grown from cuttings. The petioles were fixed at their distal ends just beneath the blades with the method described, and a short zone near the base was reduced to the median bundle together with a little surrounding parenchyma. The pots were then placed horizontal with the treated leaves on edge as usual.

In each of three plants of *Viola odorata* a young leaf of about half length was thus treated, and all three leaves twisted positively and continued to twist far beyond the normal orientation. Table 2 records the torsions at various times, and Fig. 2 shows how leaf 3 appeared at 7 days, with the degrees of torsion at various levels along its petiole. These big torsions must have been due to an influence transmitted from the continually stimulated blades, just as in *Phaseolus*.

In each of two very young seedlings of *Althaea rosea* (hollyhock) with only five leaves expanded the petiole of the youngest expanded leaf was fixed distally and tested by the new method. After only 22 hr. the treated petioles had both twisted +90°, thus reaching the normal orientation, and after that they twisted no more. So in this species the effect of the stimulus perceived locally in the petiole must be stronger than any influence transmitted from the blade.

In the remaining two species, which were chosen because their leaves seemed likely to respond especially well, the results obtained were striking but very puzzling. They are recorded in Tables 3 and 4. In those plants of both species which were tested earliest, in May 1943, the petioles of the young leaves fixed distally with the new method made negative torsions, which sometimes continued far beyond the normal orientation. But later in the summer both species made only positive torsions, which also often continued far beyond the normal orientation. Positive and negative torsions in *Lunaria* are illustrated in Figs. 3 and 4.

Table 2. *Torsions in degrees of petioles of* Viola odorata *fixed distally*

Leaf	1 day	2 days	3 days	5 days	7 days	8 days
1	+60	+135	+225	+360	+450	+495
2	+45	+150	+240	+360	—	—
3	+90	+180	+225	+360	+470	—

Table 3. Lunaria biennis. *Torsions of petioles fixed distally*

Leaf	Date	1 day	2 days	3 days	4 days	5 days	6 days	7 to 8 days
1	1 May	0	− 90	−180	−240	−200	−200	−200
2	3 May	0	− 80	− 30	− 60	−120	—	−150
3	5 May	0	− 60	− 75	− 75	− 75	− 75	—
4	10 May	0	− 70	− 80	− 80	—	—	—
5	30 June	+30	+135	+150	+170	+250	+290	—
6	6 July	0	+ 90	+135	+170	+200	+240	+290
7	12 July	0	+130	+150	+250	+360	+420	+430
8	9 Aug.	0	+ 90	+100	+170	—	—	+390
9	11 Apr.	0	+ 30	+ 60	+120	+210	+250	+290
10	14 Apr.	+80	+150	+170	—	+350	+380	—
11	20 Apr.	0	+ 30	+150	+190	+230	+300	+360
12	1 May	+60	+ 80	+100	+100	+ 30	+ 30	—
13	2 May	0	+ 70	+ 90	—	—	+ 90	—
14	3 May	+45	+ 90	—	+100	+120	—	+170

Table 4. Stachys silvatica. *Torsions of petioles fixed distally*

Leaf	Date	1 day	2 days	3 days	4 days	5 days
1	5 May	0	− 60	−180	—	−200
2	17 May	0	− 60	− 45	0	—
3	19 May	0	−200	−180	− 90	—
4	22 May	0	−135	−135	−120	− 80
5	22 May	0	−160	−190	−190	−190
6	6 June	+ 60	+ 10	+ 30	+ 30	—
7	25 June	+ 70	+100	+100	—	—
8	2 July	+ 70	+ 90	+ 90	+ 90	—
9	5 July	+ 30	+110	+180	+200	+200
10	10 July	0	+ 35	+ 60	+ 80	+ 70
11	14 July	+120	+200	+190	—	—

It was not found possible to correlate this difference in response with any difference in the manner of operating, nor in the light or temperature, nor in the age or observed condition of the leaves or plants. In case the negative torsions might have been due in some unknown way to the early season, some more plants of *Lunaria* were tested in the following April and May (nos. 9–14 of Table 3), but again they all twisted positively. In the last of these plants the basal zone of the petiole was killed with a hot glass rod instead of being reduced by cutting, since this operation had led to negative torsions in pulvini of *Phaseolus*; but still the torsion was positive and strong. It may be noticed in Table 4

that in the *Stachys* leaves several of the negative torsions (nos. 2, 3 and 4) and one positive torsion (no. 6) reached a maximum and then diminished greatly; and so too did one of the positive torsions in the *Lunaria* leaves (Table 3, no. 12). Also four of the positive torsions in *Stachys* fluctuated periodically during a few successive days, starting to do so at various times after the operations. The fluctuation of one of these (no. 6) can be seen in Table 4, and those of the other three, which were too rapid to appear in that table, are shown in Table 5. A fluctuation in a *Lunaria* leaf can be seen in Table 3, no. 2. These diminutions and fluctuations suggest that positive and negative tendencies were in conflict.

Table 5. *Fluctuations of torsions in* Stachys silvatica

	Morn	Eve	Morn	Eve	Morn
Leaf no. 9 from 5th day onwards	+200	+150	+200	+150	+170
Leaf no. 10 from 3rd day onwards	+ 35	+ 80	+ 60	+ 80	—
Leaf no. 11 from 2nd day onwards	+120	+ 90	+200	+180	+190

Since after the earliest few experiments the petioles in both these species always responded positively, it did not seem very profitable to continue testing them. The prospect would be better if a species could be found in which the distally fixed petioles could be made to twist in either direction by varying some known factor, like the pulvini of *Phaseolus*.

It is again remarkable that it was only when fixed distally that the petioles of *Lunaria* and *Stachys*, like the pulvini of *Phaseolus*, sometimes responded negatively. The petioles of normal intact leaves in the two species always respond in the positive direction only, as is also the general rule for all intact strophic organs. Since therefore the negative torsions in distally fixed petioles and pulvini favour the one kind of theory of the mechanism of torsion, and the positive torsions the other, the question arises whether actually mechanisms of *both* kinds may be at work, like the 'double assurance' mechanisms in animal development. If so, they would act in the same sense in leaves fixed basally, causing positive torsions, but in leaves fixed distally they would act in opposite senses, and some varying factor might decide which would prevail.

6. Stimulations of constrained leaves

The writer illustrated previously (1942, p. 8) sections of the rachis of a *Spiraea* leaf which had been arranged on edge and left to be stimulated for 17 days, while being mechanically prevented from twisting as a whole; and it appeared that by internal changes the cortex had twisted round in the positive direction relatively to the stele. A similar experiment has now been performed on young leaves of four seedlings of *Lunaria biennis*. The pots were placed horizontal so that the leaves to be tested were on edge, and the most distal part of the petiole, together with a little of the base of the blade, was held firmly between the lower parts of two microscope slides, which were arranged vertically and pressed together with a wooden clamp applied to their upper parts and attached to a stand. The petioles were left to be stimulated by gravity and overhead light for periods from 10 to 22 days, and were then pickled and examined in transverse sections. In all four the cortex appeared to have twisted round slightly in the positive direction relatively to the stele, and the one in which the twist was clearest is illustrated in Fig. 7.

Also in the petiole of one out of three violet leaves which were similarly stimulated the cortex was found after 14 days to have twisted slightly in the same direction. It is illustrated in Fig. 8.

Again, in nine *Phaseolus* seedlings the distal pulvinus of a young primary leaf was constrained with the same method and stimulated for periods from 7 to 17 days. The cortex was then found to have twisted in the positive direction relatively to the stele in all except one, in which no change was seen. Sections of two of these pulvini, which had been stimulated for 7 and 17 days, are illustrated in Figs. 5 and 6. The others were very similar.

These experiments indicate that it is the cortex which develops the twisting force, since the cortex twists in the normal direction in relation to the stele. But they do not provide much evidence for or against the transverse growth theory of torsion. In the hope, therefore, of obtaining such evidence, a rather different experiment was performed on *Phaseolus*, the idea being to see whether the prominent dorsal ridges of the petiole would curve when persistently stimulated, in a manner agreeing with the theory.

For this purpose, in five seedlings a very young primary leaf, of less than half length, was fixed at the distal pulvinus by the method of § 2, and also at a zone of the petiole from 1·0 to 1·5 cm. proximally to it. The pots were then placed horizontal, as usual, with the leaves so treated on edge, and were kept horizontal for periods from 12 to 16 days. The length of petiole between the fixed zones was too short to twist more than a little, so that it was continually stimulated, but it was hoped that the dorsal ridges in this region might have enough freedom to be able to curve. In three of the leaves they were given more freedom by being cut through transversely at one end or the other of the length between the fixed zones.

After the periods of stimulation the parts of the petioles between the fixed zones were pickled and sectioned transversely, and it was found that in all five the dorsal ridges had curved upwards, so that they now made various angles with the median planes of the petioles. Sections of the two petioles in which the ridges had curved most strongly are illustrated in Figs. 9 and 10. The irregular outlines of the main parts of these petioles were due to increased growth of the cortex in some parts.

The upward curvatures of the dorsal ridges agree very well indeed with the transverse growth theory, according to which a strophic organ, such as one of these petioles, is transversely polarized in such a way that its dorsal half, when stimulated, responds in the transverse plane by differential growth like that of a shoot, i.e. by growing faster on the lower side. Perhaps the drawings may make it clear that this theory deserves to be taken seriously. To complete the tests it is necessary to test similarly some geostrophic petiole or other organ possessing a prominent ridge on its ventral surface, if any such exists. According to the theory a ventral ridge should respond by curving downwards, since the ventral half of a strophic organ is supposed to respond transversely like a root.

It may be mentioned that the petioles and pulvini tested did not make any sudden or rapid torsions when released from constraint.

7. TORSIONS CAUSED BY APPLIED AUXIN

It seemed of interest to find out whether geostrophic petioles and pulvini would twist if they were given auxin on one side. For this purpose a paste of hetero-auxin in lanoline was used of strength 1 in 350, but as the crystals were several years old, the strength was only about equal to that of a 1 in 1000 paste with fresh crystals.

In nine rather young primary leaves of *Phaseolus multiflorus* seedlings, the distal pulvinus was given a streak of the hetero-auxin paste along one side. The petioles soon began to twist in the direction which carried the auxinated side of the pulvinus towards
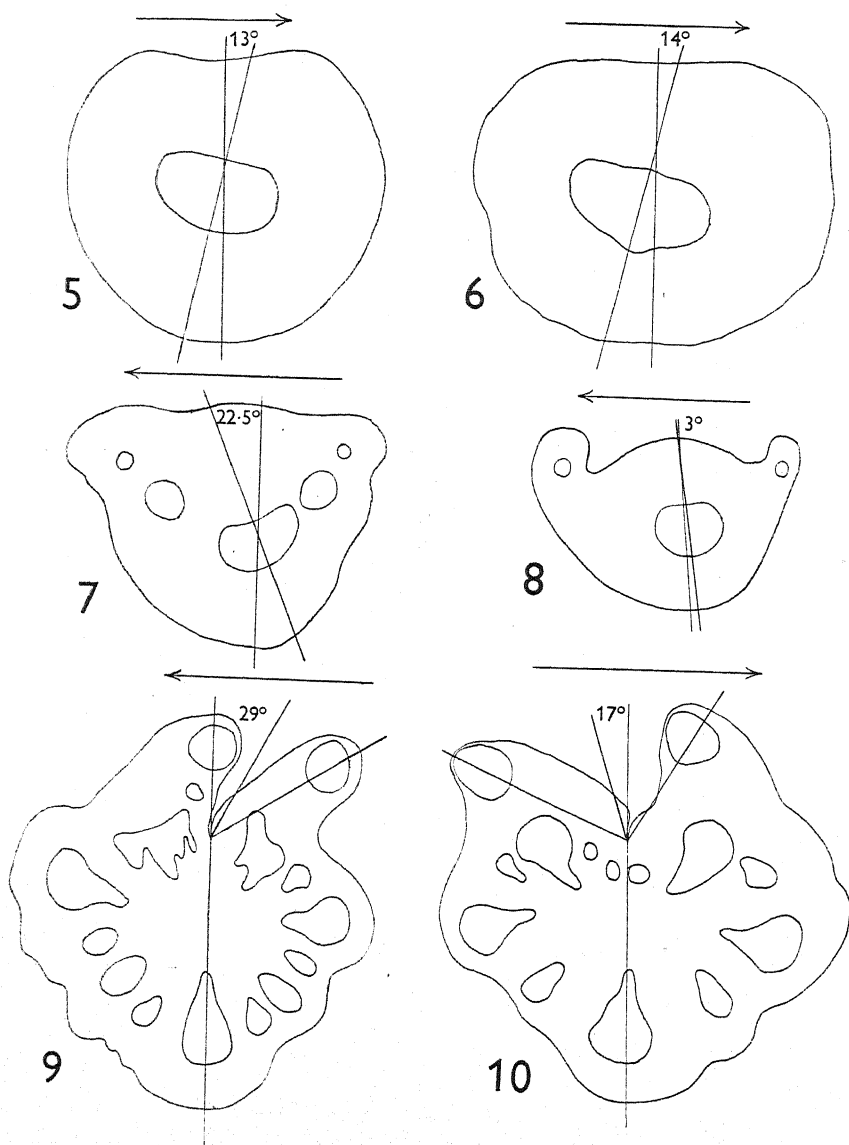
Figs. 5–10. Showing constrained pulvini and petioles stimulated on edge for many days. The arrows show the directions of the stimuli of gravity and overhead light. Figs. 5, 6. Pulvini of *Phaseolus*, ×11. Figs. 7, 8. Petioles of *Lunaria biennis* and *Viola odorata*, ×15. Figs. 9, 10. Petioles of *Phaseolus*, ×11.

the top, and after some days, when the petioles had quite stopped moving, they were all found to have twisted about 60° in this direction and to be practically uncurved. The auxinated pulvini themselves had not twisted, or scarcely. Some of the petioles had indeed already twisted in less than 12 hr., but at these earlier times they had also been

curved away from the paste from 30 to 50°, which was a complication. The curves disappeared later, but the torsions remained. Still even at the earlier times the torsions cannot have resulted from the curves, since if young *Phaseolus* petioles are bent mechanically to one side, they twist slightly in the opposite direction to that in which they twisted when the curves were due to auxin applied on one side.

In three leaves of *Lupinus albus* seedlings, of about half the final length, the distal end of the petiole was given a streak of the auxin paste along one side. After 24 hr. the petioles were twisted 90, 70 and 60° so as to bring their auxinated sides towards the top. They were also curved away from the paste 50, 30 and 20°, but the curves cannot have caused the torsions, since in this species bending the petiole to one side makes it twist only very slightly if at all.

Also the rachises of some young pinnate leaves of *Spiraea arborea* and young internodes of some plagiotropic stems of *Philadelphus coronarius*, when given auxin paste along one side, twisted from 50 to 90° so as to raise the side with the paste, though others of these leaves and stems failed to twist. The *Philadelphus* stems curved only slightly: the *Spiraea* rachises curved strongly away from the paste, but again the curvatures cannot have caused the torsions, since bending the rachis to one side makes it twist the other way, so that the convex side sinks.

The petioles of *Viola odorata*, *Stachys silvatica* and *Lunaria biennis* when given paste on one side, also twisted so as to raise the paste, but less strongly, and they also curved a little away from the paste. In these three species the curvatures may have caused the torsions, since bending the petioles to one side makes the convex side rise.

In order to interpret these torsions, it needs to be determined whether their direction depends on the position of the auxin paste in relation to the stimuli of gravity and overhead light, or on its position in relation to the structure of the organ. Is it the rule that the auxinated side of the petiole rises by torsion towards the top, or that it moves towards the position occupied previously by the dorsal face? This can be tested by applying auxin paste to one side as usual and inverting the whole plant: for then on the first hypothesis the auxinated side of the petiole should again rise by torsion, and on the second hypothesis it should sink. Naturally the possibility of ordinary geostrophic stimulation must be considered, but if the auxinated leaf is orientated accurately in the inverse position, the petiole will be in the position of labile geostrophic equilibrium. It is therefore likely to twist round one way or the other towards the normal orientation, but a tendency of the auxinated side to rise or sink will determine which way round the petiole will twist.

The test was made on *Phaseolus* seedlings, the auxin paste being applied to one side of the distal pulvinus as before, and sometimes also for a little way along the under-surfaces of the lateral veins of the blades on the same side. In order to get consistent results, it was found necessary to make sure that the auxinated leaf was orientated accurately in the inverse position at the start. For otherwise it was liable to be stimulated strongly by gravity, and the effect of the geostrophic stimulus sometimes opposed and overcame the effect of the auxin paste. So leaves were chosen that were fairly symmetric and had good straight petioles, and after the plants were inverted the leaf-blades were kept accurately horizontal for the first few hours by being supported on glass plates, until the applied auxin had had time to determine the direction of torsion.

Eight young primary leaves were tested with these precautions, and their petioles all

twisted so as to move the auxinated sides to the top. They all twisted about 90° and then stopped, the auxin paste being now on top and the leaf being on edge. Seven of the eight leaves reached the 90° within 24 hr. and four of them within 10 hr.

After 1 or 2 days more the pots were put upright, so that the auxin paste was now underneath; and thereupon in about another day the torsions all reversed and went to about 60° the other way, so that the auxin paste was brought nearly, though not quite, to the top again.

It may be noted that in all these experiments with auxin paste the distal pulvini themselves did not twist appreciably, though at first they curved away. The explanation of this is not clear, but it simplified the results.

The results show clearly that the petioles twist so as to bring the auxinated side towards the top, not necessarily so as to move it towards the dorsal surface. So the auxination of one side acts by changing the orientation of equilibrium in relation to gravity and overhead light, the new orientation of equilibrium being that in which the auxinated side is nearly on top. Thus a line along the organ somewhere between the auxinated side and the dorsum, but closer to the former, comes to act physiologically like a new dorsum. Probably this line could be brought still closer to the auxinated side, or be made to coincide with it, by applying the auxin in higher concentration. Further, since it is the side with artificially increased concentration of auxin which becomes physiologically dorsal, it seems very probable that in untreated petioles or other plagiotropic organs the normal dorsum acts physiologically as it does because it tends to accumulate the highest concentration of the natural auxin. This would also explain the tendency of such organs to epinasty; and actually Uyldert (1931, p. 51) has reported an experiment which makes it probable that in epinastic shoots of *Tradescantia* the auxin is distributed in this way.

From these results it follows that if the torsions depend on a transverse polarization in the dorsiventral plane of a kind such as Rawitscher suggests, then the polarization cannot be structurally or permanently fixed in this plane. It should be mentioned that some lateral organs are hyponastic. Perhaps in these an auxinated side would sink.

Apart from this reorientating effect of auxin applied to one side, there is a quite different general effect of auxin as one of the conditions necessary for normal strophic response in some leaves at least. For leaves of ash and of *Spiraea arborea* were found not to twist in response to stimuli of gravity and light if deprived of their leaflets, but in an experiment on *Spiraea arborea* it was found that the leaves without leaflets were still able to do so if hetero-auxin in lanoline was applied generously to the stumps of the removed leaflets and to the tip of the rachis. The leaves with neither leaflets nor applied hetero-auxin were usually still able to make epinastic and geotropic curvatures, so that apparently less auxin was needed for these curvatures than for torsions.

8. A NOTE ON THE DIFFERENCE BETWEEN THE TRANSVERSE GROWTH AND HELICAL THEORIES OF TORSION

The essential difference between the transverse growth theory of torsion and the helical theory, previously called the oblique elongation theory, can perhaps be brought out rather more clearly than in the previous paper (1942, p. 2). For the names given to these two theories may suggest that the difference between them is that according to the one the primary response to stimulation takes place in a transverse direction, and according to

the other in an oblique or helical direction. But this is not the essential difference: indeed on the transverse growth theory, although the postulated primary growth responses will naturally cause the greatest torsion if they take place exactly in the transverse direction, they will also cause torsion if they take place in an oblique direction. The essential difference is that on the helical theory the primary response is that the longitudinal growth is diverted into the direction of a helix of which the sense is determined by the direction of the stimulus. But on the transverse growth theory the primary response is not any change in the *direction* of growth at all, but a change in the *distribution* of growth in the transverse plane, such that the lower part of the dorsal half of the organ and the upper part of the ventral half grow in that plane more strongly. From these changes in the distribution of growth the torsions are supposed to follow, and these are in fact changes in the direction of growth: but on this theory they are not the primary response, but the result of changes in the distribution of growth, just as they are in the tropisms. On the other hand, the helical theory postulates something quite different from what is found in the tropisms, a change in the *direction* of growth determined as the primary response by the direction of the stimulus. Schwendener & Krabbe (1892, p. 59) do not indeed actually state that the change in direction of growth is the primary response, but they seem to imply this, since they do not suggest that it may result from any other primary response.

9. Conclusions

It had been hoped to decide between the two main theories of the mechanism of torsion by means of the experiments on leaves fixed distally. But actually in these experiments although positive torsions predominated, supporting the transverse growth theory, yet negative torsions were sometimes obtained in the pulvini of *Phaseolus* and in the petioles of *Lunaria* and *Stachys*. In the pulvini they were obtained when the leaves were not in organic continuity with the rest of the plant, and in the petioles in conditions which unfortunately could not be determined. These negative torsions have been briefly discussed at the ends of §§ 4 and 5, and further work is needed to interpret them. They indicate that the mechanism of torsion must be complicated.

However, evidence clearly tending to support the transverse growth theory was obtained in the experiments on constrained leaves reported in § 6. As to the re-orientating effect of auxin paste applied to one side of a petiole or pulvinus, further work is needed to discover whether a connexion can be found between this effect and the transverse growth theory.

Summary

1. A method is described for fixing leaves distally, and setting them free to twist at the base by reducing a basal zone of the petiole to a thin conducting strand. The purpose was to see in which direction the parts proximal to the fixed zone would twist when the leaves were placed on edge. The direction of torsion which *at the start* tends to bring the correct face uppermost will be called positive.

2. The rachises of the pinnate leaves of *Spiraea arborea* thus treated twisted 90° positively.

3. The distal pulvini of leaves of *Phaseolus multiflorus* thus treated twisted positively up to 200°. But in *detached* leaves fixed distally they twisted negatively as before (Snow, 1942). When connected with the plant by a basal dead zone, they twisted feebly negatively, if at all.

4. The young petioles of *Phaseolus multiflorus*, *Viola odorata*, and *Althaea rosea* similarly treated with the new method twisted positively, in *Viola* up to 495°.

5. The young petioles of *Lunaria biennis* and *Stachys silvatica* usually twisted positively, and often far beyond 90°. But sometimes they twisted negatively, and again sometimes far beyond 90°.

6. In pulvini of *Phaseolus* and petioles of *Lunaria* which were stimulated on edge for many days while mechanically prevented from twisting as wholes, the cortex appeared to have twisted positively in relation to the stele.

7. In young petioles of *Phaseolus* fixed at two neighbouring zones and similarly stimulated, the dorsal ridges in the part between the fixed zones curved upwards in a manner agreeing well with Rawitscher's transverse growth hypothesis (1932).

8. The petioles of young intact leaves of various species, if given hetero-auxin on one side, twist so as to bring the auxinated side nearly to the top. In *Phaseolus* this was shown to happen also when the whole plant was inverted. So the direction of the torsion after auxination is determined in relation to the direction of the stimuli of gravity and overhead light, and the auxinated side becomes physiologically dorsal.

9. The interpretation of the results is discussed in the various sections.

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STUDIES IN ATMOSPHERIC POLLEN

II. DIURNAL VARIATION IN THE INCIDENCE OF GRASS POLLEN

By H. A. HYDE and D. A. WILLIAMS

National Museum of Wales and Llandough Hospital, Cardiff

(With 5 figures in the text)

CONTENTS

1. INTRODUCTION

It was shown in a previous paper (Hyde & Williams, 1944) that in the aggregate grass pollens formed 75 % of the total pollen deposit caught at Llandough, Cardiff, during the months of June and July 1942, and that the daily deposit of these pollens even at the height of the season fluctuated very widely indeed. Counts of 100 grains or more per 5 sq.cm. were obtained over a period of $6\frac{1}{2}$ weeks from 6 June until 20 July inclusive; but while 7 days gave over 300, 9 days gave under 50; and the highest and lowest counts (482 on 23 June and 7 on 18 June) were obtained within a few days of each other. Consideration of weather data showed that during the period concerned sunny weather was conducive to the deposition of large quantities of grass pollen and suggested that further observations might elucidate the relationship. We describe here the results of experiments we have made partly to this end, but partly also to serve a purely utilitarian purpose: we wished to find out whether the grass pollen in the air varied in any predetermined manner from one time of day to another, and if so to what extent, so that if possible hay-fever patients might be advised accordingly.

Very few observations seem to have been made on diurnal periodicity of grass-pollen incidence, and when we began the present study we knew of none. We have since read Rempe's paper (Rempe, 1937) in which he describes *inter alia* the changes, during the course of a single period of 24 hr., in the concentration of rye (*Secale cereale*) pollen as measured by the number of grains caught during successive 2-hourly periods on a vertical adhesive surface exposed at the height of the ears (1·85 m. above ground-level). He made no attempt, apparently, to study changes in the rye pollen catch in relation to weather conditions.

Our experiments fall into two main series, which were carried out at Llandough, Cardiff, in 1943 and 1944 respectively. Essentially they consisted in exposing prepared slides to catch pollen, the slides being changed 2-hourly instead of daily, while simultaneous observations were made on the weather, and (in 1944), on the flowering of the grasses growing near the apparatus. In 1943, Dr John Freeman also exposed a short series for us on the roof of St Mary's Hospital, Paddington.

2. PRELIMINARY INVESTIGATION: THE 1943 EXPERIMENTS AT LLANDOUGH

The pollens were caught, as in 1942, by the gravity slide method. The apparatus used, however, was simpler than that previously described. It consisted (Fig. 1) essentially of two horizontal asbestos disks $2\frac{1}{2}$ ft. in diameter bolted together so that the one was
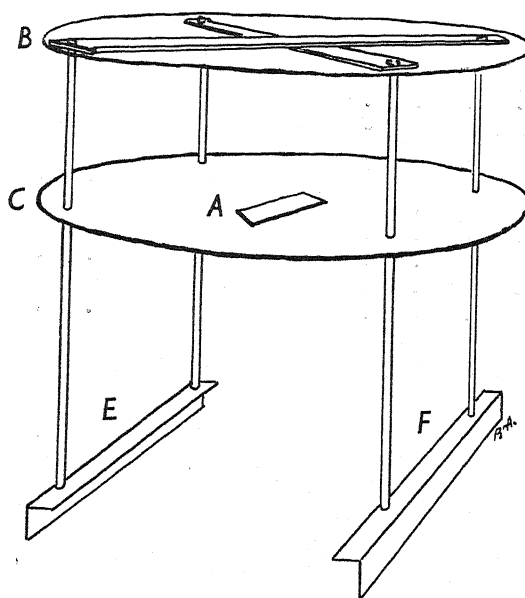
Fig. 1. Apparatus used for exposing slides to catch pollen. The slide *A* rests on the lower asbestos board disk *C* (to which it is attached by adhesive strapping) and is protected from rain by the upper disk *B*. The two disks are held together by four vertical bolts which in turn are sunk into the steel girders *E* and *F*. Diameter of disks, 36 in. = 91·5 cm. Vertical distances: *BC*, 11 in. = 28 cm.; *C* to ground or roof respectively, 12 in. = 30·5 cm.

superimposed 11 in. above the other. The lower was 12 in. above the ground (or roof projection) and the slide was placed on this disk and held in position by a thin strip of surgical strapping. This simple device, while protecting the slide from all but the most violent squalls, allowed air currents to pass freely over the adhesive surface.

The general surroundings of Llandough Hospital have already been described (Hyde & Williams, 1944). The distribution of grassy vegetation around the building is indicated in Fig. 2. Slides were exposed at two sites, one (*A*) on the roof of the operating theatre, the other (*B*) on the ground just outside the Hospital. Site *B* (marked *B* in the figure) was a patch of made ground which had been levelled when the Hospital was built in 1933 and had been allowed to become colonized naturally. Grasses predominated in the vegetation (see Table 1), but other species occupied a good deal of the ground.
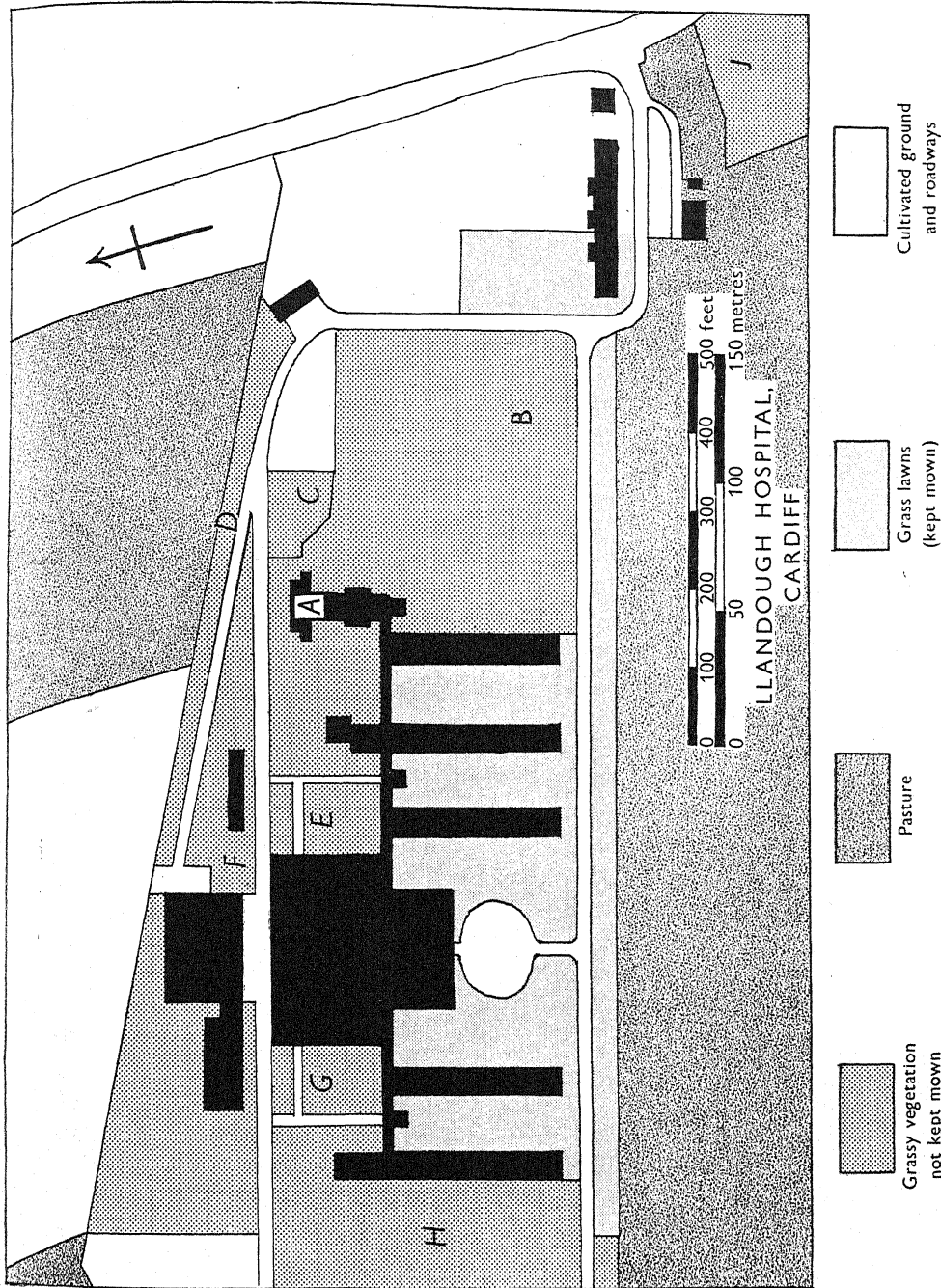
Fig. 2. Llandough Hospital and grounds. Sketch map to show sites occupied by apparatus and areas of grassy vegetation. *A*, site of apparatus on roof, 1941 onwards; *B*, site of apparatus on ground, 1943; *C*, ground site, 1944; *D*, *E*, *F*, *G*, *H*, *J*, various areas of grass or grassy vegetation not kept mown, 1944.

Owing to the indisposition of one of us (H. A. H.) at the time no botanical observations were made until 21 July, but observations made in 1944 point to the strong probability that by 28 June *Festuca rubra* had finished flowering in the area immediately concerned, and that the *Agrostis* had not yet come into flower: the main grass concerned was *Holcus lanatus*.

Site *B* was not perhaps ideal: its relatively thin grass covering produced only a low pollen concentration; yet this, as the event showed, was sufficient to give very significant results.

The experiment was begun at 08.00 hr. Greenwich mean time on 28 June and continued without a break until 08.00 hr. on 2 July. During the first 24 hr. slides were exposed at site *A* only, but during the remainder of the time slides were exposed simultaneously at the two sites. The usual precautions were taken to prevent contamination of the slides both before and after exposure: in particular, they were mounted as soon as possible after their removal from the apparatus. Weather observations also were made 2-hourly during the greater part of the time. The slides were afterwards analysed for grass pollens and non-grass pollens only.

Graphs showing the 2-hourly variation in rate of grass-pollen deposition at the two sites are reproduced in Fig. 3, whereon the hours of bright sunshine also appear.* This experiment could only be regarded as an exploratory one; the vegetation around the apparatus on the ground was rather thin, and no observations were made on flowering; moreover, it was a little late in the season, viz. after the summer solstice. Nevertheless, a periodicity in pollen deposition is apparent in the curves from both sites; on the whole, maxima and minima of deposition occur at the same time in both, and high and low rates of daily deposition appear to be related to long and short daily sunshine totals respectively.

The simplest explanation of the shape of the curve obtained from site *B* is that it represents pollen which has drifted directly from the flowers around on to the slide. If, then, oscillations in the catch be taken to represent changes in the atmospheric pollen concentration, these, in their turn, must depend on changes in the rate of pollen liberation from grasses on the spot. Furthermore, the correspondence between the 'roof' curve (site *A*) and the 'ground' curve (site *B*) seems to be most easily explained if one assumes that the 'roof' pollen also is derived directly from supplies which have drifted in from surrounding areas of grass. The lower values at site *A* would follow from the sedimentation of a large proportion of the pollen under the action of gravity.

It had been previously suggested to us by Prof. T. J. Jenkin (*in litt.*) that the fact that different grasses flower at different times of day should be borne in mind when attempting to interpret the curves of *daily* grass-pollen precipitation which we had obtained in 1942 (Hyde & Williams, 1944). This evidently applied with even greater force to curves resulting from 2-hourly exposures, and we attempted to correlate our curves (Fig. 3) with published observations (summarized by Beddows, 1931) on the times of flowering of the grass species noted at site *B*. These observations seemed to indicate that a maximum of pollen liberation might be expected during the morning

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* The bright sunshine records, which have been supplied by the courtesy of the City of Cardiff Public Health Department, were made at the Meteorological Station, Penylan, which is situated at 202 ft. alt. about 4¼ miles north-north-east of Llandough Hospital. Visual observations made simultaneously by us at the Hospital showed that during the period concerned the hours of bright sunshine were substantially the same at Penylan and Llandough. No rainfall was recorded.

Grains per
5 sq. cm. surface

25,000

20,000

27,900 32,500

15,000

10,000

5000

0
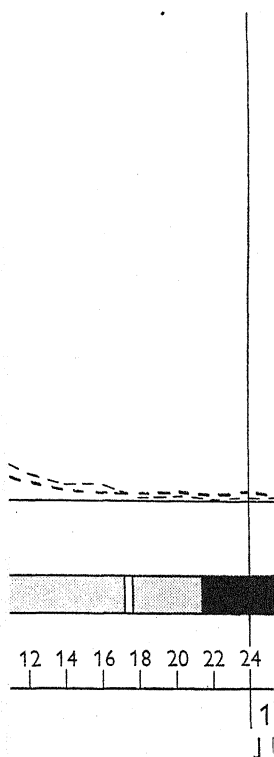
grass' vegetation), 28 June–
number of grains per 5 sq.

Holcus lanatus   +++
Festuca rubra
Dactylis glomerata
Arrhenatherum
    elatius

Sun, Cloud
& Darkness

Wind

Rain   0·15 in.

Hour   08 10 12 14 16 18 20 22 24 02 04 06 08 10 12 1
G.M.T.
Day   15   16

12 14 16 18 20 22 24

1
J
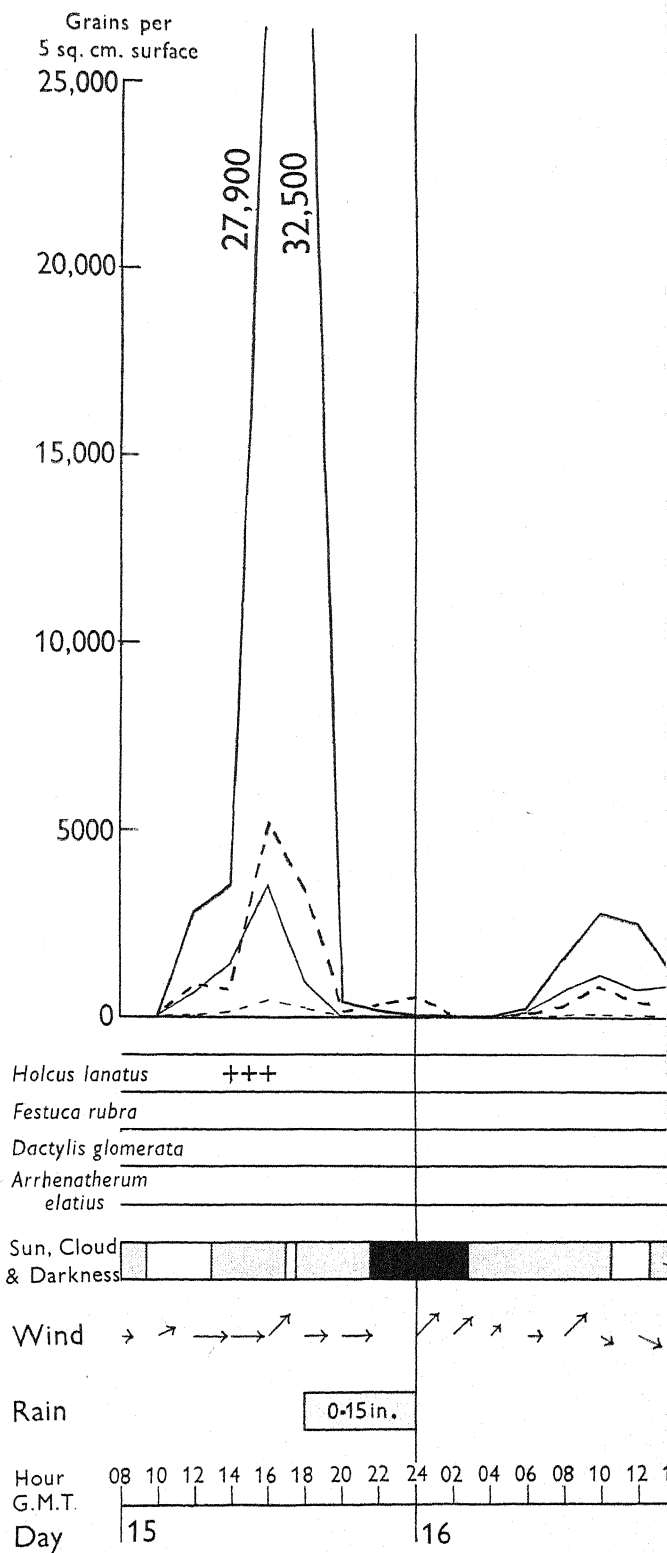
Fig. 5. Graphs of pollen catch (gravity and impact) obtain
Below: quantitative flowering

Daily periodicity in grass-pollen deposition
and 'impact', near ground and on roof.
Cardiff, 15—22 June 1944

+++   +

+

+

+++

+

12 14 16 18 20 22 24 02 04 06 08

22
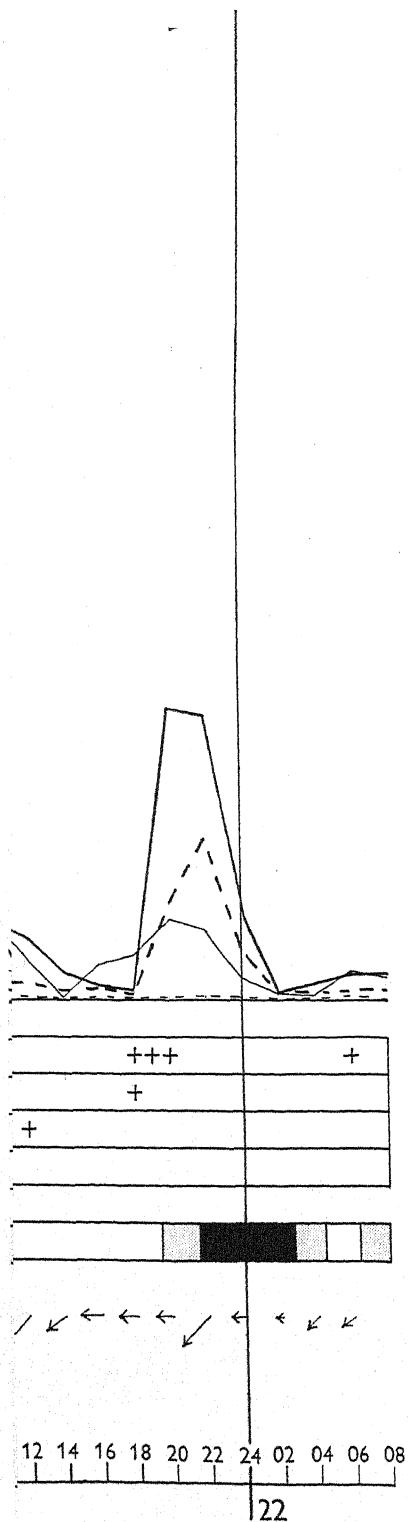
one-tenth that used in Fig. 3.)
t.

hours: we had found that on the three sunny days (28 and 29 June and 1 July) there was a maximum of deposition during the evening, viz. about 18.00 hr. G.M.T. Apparently we had to explain a time lag of at least 6 hr. between liberation and deposition. We decided therefore to make further experiments in 1944, this time with concurrent observations on the grasses concerned.

3. MAIN INVESTIGATION: THE 1944 EXPERIMENTS AT LLANDOUGH

(a) The pollen-catching experiments

The 1944 experiments and observations were made over a period of 7 days immediately before the summer solstice, viz. from 08.00 hr. on 15 June until the same hour on 22 June. Four sets of slides were exposed, two gravity slides, one on the theatre roof (site *A*) as in 1943, the other in the middle of a dense patch of purely grassy vegetation to the east of the theatre block (site *C*, Fig. 1) and two slides which were exposed in a vertical position at sites *A* and *C* respectively.
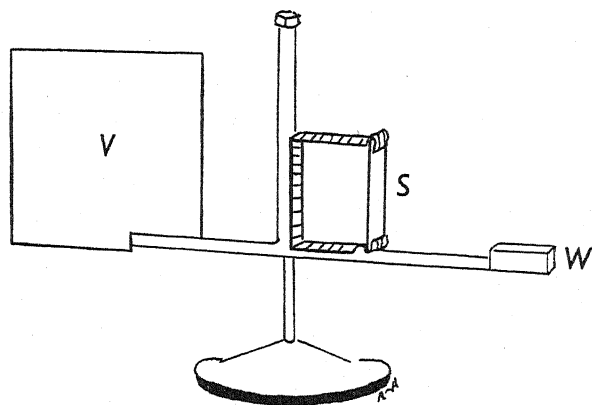
Fig. 4. Apparatus used in 1944 to hold 'impact' slides. *S*, slide held vertically in a metal clip; *V*, wind vane; *W*, counterpoise. For further explanation see text.

Each of the vertical slides (Fig. 4) was held in a metal clip attached to one end of a metal bar which carried a wind vane at the opposite end and was pivoted centrally, so that it moved freely bringing the slide to face into the wind. The pollen grains were therefore caught by impinging on the adhesive surface of the slide, hence the expression *impact* slide in contradistinction to gravity slide.* The rotating slide carrier complete was placed in the centre of the lower disk (Fig. 1). The gravity slides were exposed in the same way as in the previous year.

Site *C* was selected as being the largest area of purely grassy vegetation within easy reach of an observer whose task it was to change the slides at the two sites within as short a time as possible, and also to record the state of the weather. The site is described more fully in § (c) below.

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* In order to test the efficacy of this apparatus as a means of presenting the slide to the wind and so securing as high a catch as possible, we exposed also during the whole of the experiment a slide placed back to back with the one facing the wind. Pollen counts covering the first twenty-four 2-hourly periods showed that the catch on the slide facing backwards was consistently of the order of 1/50, or less, of the impact catch proper. We therefore concluded that the apparatus was actually functioning as desired.

The general procedure in regard to the exposure of and subsequent work on the slides was the same as that already described for the 1943 experiment, the only departure from our usual practice being necessitated by the very large quantities of pollen caught on certain slides. Thus the impact slide exposed at site C from 14.00 until 16.00 hr. on 17 June was seen to be yellow all over with pollen and to have caught a considerable number of anthers also. It was not practicable to count the whole of this and similar slides: an aliquot part of the area, viz. one-quarter of the depth of each traverse only was counted and was assumed to be a true sample.

(b) Weather conditions

The following observations were made 2-hourly, i.e. at the same times as the slides were changed: (i) state of the sky: sun shining or not; cloud extent and apparent density; wet or fine; (ii) wind direction and velocity on the Beaufort Scale. We have also made use of sunshine and rainfall records obtained in Cardiff.*

The hours of bright sunshine are set out in Fig. 5. The only appreciable rainfall during the experiment occurred between 18.00 hr. and midnight on 15 June, during which time 0·15 in. of rain was registered at Penylan Meteorological Station. Unfortunately, the wind at the time was moderate to fresh, so that a certain (unknown) proportion of the pollens caught on the impact slides must have been washed off again; the gravity slides were less affected. (It is noteworthy that the total catch during the 4 hr. after the rain stopped (165) was considerably lower than that during any other similar period in the course of the experiment (the next lowest being 385 at 00.00–04.00 hr. on 17 June). It seems fair to infer that the rain had washed the air for the time being clear of pollen. Similar results were reported by Rempe (1937).)

(c) Observations on the grasses concerned

The grasses which were noted in flower at various points around the Hospital at the time of the experiment are listed, together with rough estimates of their relative frequencies and their times of flowering in Table 1. In order to form an accurate estimate of the vegetation at site C six 1 m. quadrats were set out immediately after 22 June in a 5 yd. circle around the apparatus, and the grasses therein were mown and systematically analysed head by head. The results of this analysis (Table 2) show that, as measured in terms of heads counted, *Holcus lanatus* formed three-fifths of the total grass population in flower at the time of the experiment, and *Festuca rubra* a further quarter, while *Cynosurus cristatus*, *Dactylis glomerata*, *Lolium perenne* and *Poa trivialis* in approximately equal proportions made up the rest.

Observations on the flowering of these species of grasses were made during and after the week of the experiment. For various reasons it was not always practicable to watch the actual plants at Llandough. Supplementary observations were made therefore by one of us (H. A. H.) at two similar sites both within a few miles of the Hospital. Whenever the sets of observations were cross-checked they were always found to be in substantial agreement. The times of flowering of the more important grasses are indicated graphically at the foot of the pollen curves in Fig. 5.

* See footnote to p. 86.

Holcus lanatus flowered in quantity at Llandough in the afternoon or evening on 15, 17, 19, 20 and 21 June and much less abundantly on 18 June. There was slight flowering in the morning between 05.00 and 06.00 hr. on 19 and 22 June. These field

Table 1. *Principal grasses observed around Llandough Hospital, 1944*

Site reference in Fig. 2	B	C	D	E	F	G	H	J	Time(s) of flowering Cardiff 1944 (hr. G.M.T.)
Agrostis stolonifera var. *stolonifera**	f.	a.	—	o.	—	—	—	—	Not observed
A. alba var. *latifolia**	—	—	—	o.	—	—	—	—	Not observed
Arrhenatherum avenaceum	o.	—	d.	l.a.	—	f.	a.-d.	—	07.00–08.00
Briza media	—	—	—	o.	—	—	—	—	Not observed
Bromus mollis†	—	o.	—	—	—	—	—	v.a.	a.m.
Cynosurus cristatus	f.	f.	—	l.a.	f.	—	—	f.	05.00–06.00
Dactylis glomerata	o.	f.	—	l.a.	—	v.a.	a.	o.	Various
Festuca pratensis	—	—	—	f.	—	—	—	—	08.00–14.00
F. rubra	f.	v.a.	—	f.	v.a.	—	—	o.	(05.00–06.00); 14.00–19.00
Holcus lanatus	f.	v.a.	—	l.a.	—	—	—	—	(04.00–06.00); 14.00–18.00
Hordeum nodosum	—	o.	—	—	o.	—	—	—	13.00–14.00
Lolium perenne	f.	f.	—	f.	o.-a.	f.	—	f.	05.00–06.00; 11.00–13.00
Poa pratensis	—	o.‡	—	o.	—	—	—	o.	Not observed
P. trivialis	—	f.	—	l.a.	—	v.a.	—	f.	a.m. and p.m.
Trisetum flavescens	—	o.	—	o.	—	—	—	f.	a.m. (before 08.00)

* Did not flower in 1944 until after experiments concluded.

† Flowering completed before 15 June.

‡ Noted here though not in the quadrats.

Notes on areas lettered as above. B: 1943 apparatus, 'poor grass'; C: 1944 apparatus, 'good grass'; D, E, F, G, H: various areas of grassy vegetation adjoining the Hospital buildings; J: a meadow (not mown until after 22 June).

The letters in columns B–J indicate the degree of frequency of the species on the following scale: d. dominant; v.a. very abundant; a. abundant; l.a. locally abundant; f. frequent; o. occasional.

Table 2. *Botanical analyses of six 1 m. quadrats situated around site C*

	Heads collected in quadrats numbered respectively:						Totals	Average per m.^{2}	% of total grasses flowering
	1	2	3	4	5	6			
Cynosurus cristatus	10	17	7	102	12	32	180	30	3
Dactylis glomerata	97	6	14	15	77	2	211	35	4
Festuca rubra	282	84	6	213	547	79	1211	202	25
Holcus lanatus	661	716	550	526	89	191	2733	453	58
Hordeum nodosum	5	—	—	—	—	—	5	1	(0·001)
Lolium perenne	10	49	41	60	15	45	220	37	5
Poa trivialis	—	55	44	66	—	59	224	37	5
Trisetum flavescens	—	9	3	2	—	—	14	2	(0·002)
Total heads flowering	1065	936	665	984	740	408	4798	799	100
Bromus mollis*	14	4	17	36	—	—	71	12	0
Agrostis stolonifera†	241	196	242	230	122	724	1755	292	0
Total heads collected	1320	1136	924	1250	862	1132	6624	1104	—

* Finished flowering before experiment begun.

† Had not begun flowering when experiment concluded.

observations were confirmed by naked-eye examination of the pollen slides from site C before mounting, when *Holcus* anthers were found, in numbers roughly corresponding to its abundance of flowering, on slides exposed some hours later (usually) than the flowering times recorded. Beddows (1931), summarizing other workers' observations

on this species, says: 'It is evident that *H. lanatus* exhibits diurnal periodicity, but this is not very clearly defined.' Our experience agrees more nearly with that of Körnicke (1885, p. 199), whose results may be paraphrased by saying that *H. lanatus* has its principal flowering in the afternoon after 15.00 hr. while a much weaker flowering may take place early in the day. The main flowering at Cardiff takes place between 16.00 and 18.00 hr.; it may be postponed if the morning is dull and sun supervenes later; or in unfavourable weather it may be suppressed altogether.

Festuca rubra flowered in quantity in the afternoon or evening on 17 (14.00–19.00 hr.), 19 and 20 June and for a shorter period and also in less quantity on 21 June. Some morning flowering took place on 18, 20 and 21 June. Flowering at site *C* was confirmed by the presence of anthers on the slides at the appropriate times. The populations on which our observations of flowering were made were not all taxonomically identical. Dr W. O. Howarth, to whom we submitted gatherings from the three stations above referred to, identified varieties *vulgaris*, *glaucescens* and *dumetorum*. In regard to specimens from the uniform population at site *C*, Dr Howarth, who first placed them under var. *vulgaris*, wrote in a postscript 'fresh material might prove these to be var. *glaucescens*'.* Jenkin (1924) states that on very fine days in 1921 under cool greenhouse conditions *Festuca rubra* (variety or varieties not specified) began to flower at 09.45 hr., experienced a maximum between 12.00 and 13.00 hr. and completed its flowering at 14.30 hr. The discrepancy between his observations and ours may be due either to difference of conditions or to genetic differences in the plants.

Dactylis glomerata was observed in flower at various times, usually in the morning but once in the evening, though it flowered in mass only once, viz. on 18 June at 06.00 hr.; on this morning all the heads were covered with turgid stamens, which shed their pollen in clouds at the slightest touch.

Arrhenatherum elatius, though not represented at site *C*, dominated certain areas near the Hospital including one very near site *C* (Fig. 2, *D*). Mass flowering was observed between 07.00 and 08.00 hr. on 13, 14, 18, 20, 23 and 25 June: little or no flowering occurred on other days between these dates and none at other times of day. The heavy flowering on 18 and 20 June coincided with a marked morning rise in the pollen catch.

(d) *Correlation of pollen counts with observations on weather and grass flowering*

Examination of the four curves in Fig. 5 and of the other concurrent observations shows that:

(i) All four curves move up and down in unison: in particular no time lag between ground and roof catch is apparent.

(ii) The impact catch is almost always greater than the gravity catch on the same site.

(iii) A morning and an afternoon rise are observable at both sites every day; the afternoon rise was much the greater every day except on 16 and 18 June.

(iv) The highest maxima, especially those on the impact slide exposed near the ground (site *C*), occur following several hours of bright sunshine. On those days (16 and 18 June) when little or no bright sunshine was recorded, the afternoon rise in the pollen catch was relatively slight. On the one day (21 June) when bright sunshine did not occur until noon, but continued thereafter for several hours, there was a very marked rise but it occurred some 3 or 4 hr. later than usual.

* He added: 'There is a suggestion of bloom on some of the spikelets of the dried material.'

(v) The variations in the pollen catch at site C are closely related to the times of flowering of the principal grasses around the apparatus. The variations at site A are much less marked. It is noteworthy that when a marked rise occurs other than at the principal flowering time for *Holcus* and *Festuca rubra*, such a rise can be related to an outburst of flowering by one of the grasses near the two sites: this applies notably to the rises around 08.00 hr. on 18 and 22 June. The low catch during the hours of darkness may obviously be correlated with the total cessation of flowering during that period.

(vi) The exceptionally high catch which was obtained on 17 June followed a sunless day on 16 June; it may have been due to a holding back of anthesis on the dull day and its release the day after.*

To sum up: we have observed a diurnal variation in grass pollen incidence which can be correlated closely both in frequency and in amplitude with the incidence of bright sunshine and with the flowering of the neighbouring grasses.

4. The Paddington experiment (1943)

Gravity slides changed at 2-hourly intervals were exposed for two 24 hr. periods on 21 June and 18 July respectively in an apparatus, similar to the one described in § 2 (above), which was placed on the roof of the Department of Immunology, St Mary's Hospital, Paddington. This building, the highest in the neighbourhood (roof level 80 ft. above ground), is situated in a completely built-up neighbourhood in central London. The area is, however, by no means devoid of vegetation; there are gardens at intervals between the Hospital and Hyde Park (650 yd. = 600 m. approx. away), and the latter is largely grass clad.

To judge from reports of weather at Greenwich,† 21 June was a sunny day (11·3 hr. of bright sunshine), 18 July for the most part a dull one (3·0 hr.). The total pollen catch on 21 June was 77, that on 18 July only 51. The pollen counts in the morning (13 between 08.00 and 10.00 hr.) and in the evening (24 between 18.00 and 22.00 hr.) on 21 June were strikingly higher than at other times on either of the 2 days, but the numbers throughout are so small that we hesitate to suggest the occurrence of any periodicity.

5. Discussion and conclusions

(a) Pollen liberation and dispersal in grasses

Comparison of the two curves from site C (Fig. 5) shows that, while both appear to give some measure of the grass-pollen liberation at that site, the impact catch is clearly the more sensitive index of the process. The grasses mainly concerned are typically chasmogamous in habit and there is abundant evidence that anthesis in such grasses takes place at very definite times of day. Our results show further that given favourable conditions, pollen liberation in chasmogamous grasses takes place in very large quantities during a relatively short period or periods each day, and that between times little or no pollen is set free. Field observations on the numbers of plants seen in flower from time to time and also on the dehiscence of, and liberation of pollen from, individual anthers, and subsequent laboratory examination of these anthers all bear out this conclusion.

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* A similar explanation may apply to the high catch on 1 July 1943. Prof. Jenkin informed us that this is what, from his experience in breeding work on grasses, he would expect.
  † Supplied by the courtesy of the Director, Meteorological Office, Air Ministry.

(It so happened that the grasses on which our principal observations were made flowered mainly in the afternoon. This was unexpected and seems to be exceptional.)

One of the most striking features of the graphs (Figs. 3 and 5) is the simultaneous occurrence of maxima at the paired sites under observation (*A* and *B* in 1943, *A* and *C* in 1944). It is evident that grass pollen liberation rapidly affects atmospheric pollen concentration in the surrounding neighbourhood; and it is equally evident that in general the effect is short-lived: in the absence of local liberation atmospheric concentration in general rapidly falls to a very low level. Some grass pollen, it is true, continued to be caught at site *A* even during the hours of darkness: this may or may not have been carried from a distance.

Rempe (1937) exposed adhesive surfaces to catch pollen at various altitudes during a series of aeroplane flights. He was thus able to prove that during the daytime, under certain weather conditions which often occur, large quantities of pollen are borne by upward currents to a height of 2000 m. (6600 ft.), while during the night hours a very marked sedimentation takes place. He concluded that given moderate wind velocities (say 5 m. per second, or just over 11 miles an hour) more than one-third of the whole amount of pollen in the air may be transported over a distance of 300 km. (say 190 miles) or more. He found further that on the roof of the Botanical Institute at Göttingen during the period 1 to 31 May 1935 the pollen catch by deposition during the night hours (7.30 p.m. to 7.30 a.m.) made up 37·8% of the total, while that by impact during the night made up only 16·6% of the total, and considered that these results bore out his contention of the relative importance of sedimentation at night. We have extracted for comparison (see Table 3) our figures relating to catch by deposition and impact respectively on the roof of the Hospital (site *A*). We do not find that the percentage nightly gravity catch over a period of 6 days is significantly greater than the corresponding proportion of the impact catch and our day to day figures consistently agree in this respect.

Table 3. *Comparison of pollen impact catch and pollen deposition (grains caught on 5 sq.cm.) on the roof of Llandough Hospital (site A) in the daytime and at night during the 6 days from 06.00 hr. on 16 June until 06.00 hr. on 22 June 1944*

	Impact catch	Gravity catch
Day 06.00–18.00 hr. Night 18.00–06.00 hr.	44,949 24,975	4,373 2,625
Day + night	69,924	6,998
Nightly catch as percentage of 24 hr. total	35·7	37

The disagreement between our figures and Rempe's is probably to be explained by the fact that, whereas his pollen catch was predominantly tree pollen, we are concerned here only with grass pollen. It was shown by Schmidt (1918, 1926) that pollen grains and other particles of a similar size, which, if affected only by horizontal air currents, would all fall to the ground at a distance easily computable from Stokes's law, are likely, as the result of atmospheric turbulence, to be borne, though in rapidly diminishing proportions, to a much greater distance. This effect, which Schmidt called *Austausch*, increases rapidly from ground level upwards: it is to be expected therefore that grass

pollens, which are liberated into conditions of smaller *Austausch* than are tree pollens, will have less chance of being brought under the influence of vertical air currents and thus being carried high into the air. If they are not carried up in quantity during the day they will not be sedimented largely at night; and in practice we do not find any relative increase in deposition as compared with impact at night.

If the above line of argument is sound we should expect to find that distant transport of grass pollen is inconsiderable (the Paddington figures are consistent with this view) and much less than that of tree pollens. We hope that the widespread observations on pollen deposition made by us in 1943 will throw further light on this question.

(b) *Grass-pollen concentration in relation to allergy*

The most important practical conclusion to be drawn from our results by allergists is that in the neighbourhood of grassy vegetation grass-pollen concentration in the atmosphere varies enormously according to the time of day and the weather conditions. During the midnight hours, even during fine weather at the height of the grass season, it may be very low indeed. On the other hand, at certain times, dependent on the flowering habits of the dominant grasses, the pollen concentration rises to previously unsuspected levels. At Llandough, just after midsummer on fine sunny days, maximum values are attained in the late afternoon; on dull days no such rise occurs. In other localities where the principal grasses flower in the early morning the maximum pollen incidence is likely to occur at that time of day, provided that the air is not too still; the intensity of flowering may, however, be affected by the amount of sunshine received on the previous day.

The study of atmospheric pollen has received much attention in the U.S.A. American workers generally have used 24 hr. gravity slides in an attempt to determine the amount of pollen in the air from day to day. Doubtless such slides are of value as giving a general indication of pollen incidence, though the figures so obtained, so far as they concern grasses, should be read in the light of the facts stated in the last paragraph. Certain investigators, however (cf. Cocke, 1937), have used daily counts of gravity slides as a basis for computing atmospheric pollen concentration in grains per unit volume, assuming the grains to be free to fall vertically in accordance with Stokes's law. The resulting figure is at best only an average for the whole 24 hr. period and our experiments show that so far as grasses are concerned it can have no real meaning.

6. SUMMARY

1. The atmospheric concentration of grass pollen, as measured in terms of the catch on adhesive slides exposed continuously and changed 2-hourly, has been studied at stations sited in the middle of grassy vegetation and on a building at a short distance therefrom, and has been related to the times of flowering of the principal grasses concerned and to the weather conditions experienced.

2. On fine sunny days the principal grasses (*Festuca rubra* and *Holcus lanatus*) flowered as a rule slightly in the morning but profusely in the late afternoon.

3. Pollen liberation was crowded into a short period following mass anthesis: local pollen concentration rose and fell correspondingly, without any perceptible lag.

4. On dull days anthesis was largely suppressed and local pollen concentration remained low.

7. Acknowledgements

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REVIEWS

Plant Viruses and Virus Diseases. Second edition. By F. C. BAWDEN. $6\frac{7}{8} \times 10\frac{1}{4}$ in. Pp. 294, with 1 plate and 48 text-figures. Waltham, Mass.: The Chronica Botanica Co.; London: Wm. Dawson and Sons, Ltd. 1943. Price $4.75.

Progress in the study of plant viruses during the last decade has been rapid, and the author of this book has been associated intimately with much of the research on which present-day conceptions of the nature of viruses are based. It was inevitable that the first edition of this book, published in 1939, should have become out of date very rapidly, and the author has wisely taken advantage of the necessity of resetting all the type, due to the German invasion of the Netherlands where the first edition was published, to rewrite and rearrange much of the subject-matter, including references up to 1941 and much work from the author's laboratory which has been published since that date. Many new illustrations are also included, among them photomicrographs of several of the tobacco necrosis viruses isolated and purified at Rothamsted.

It is not long since viruses were regarded as somewhat nebulous infectious fluids, and the discovery that some at least of the plant viruses were large nucleoproteins came as a surprise to many. Indeed, much energy has been devoted to attempts to disprove the molecular nature of some viruses. However, it has proved possible to distinguish between strains of certain viruses even in the proportions of the various amino-acids in their composition and by differences in their antigenic structure. All plant viruses isolated so far have proved to be proteins and by analogy it is usually assumed that all viruses are as simple, although this is by no means the case among animal viruses. Methods of isolation and purification which have been developed up to the present, and which are only suitable for studies on exceptionally stable or infectious viruses, are described in detail. It may be said that undue space is devoted to the description of salt precipitation methods, which are known in many cases to cause alterations in the properties of the viruses, compared with that given to the account of the equally useful and less drastic centrifugal methods developed in America.

As may be expected, the classification of viruses, even of a provisional type, presents great difficulties, as, owing to the wide host range of some of them, several have been described under different names and on different hosts. Systems based on symptomatology have the defect that a virus may show almost any symptom picture depending upon the host plant and even upon the weather, while those based on the common host range are purely artificial and fail to disclose any relationships between the viruses themselves. Serological studies have revealed unsuspected relationships between viruses having no common host plant, and in combination with the physical and chemical properties of the viruses themselves, would provide a sound basis for classification. Unfortunately, this elegant method is limited to a few viruses, and confusion has already resulted from the use of impure antigens for antiserum production. Certain mixtures of viruses or strains of the latter are also very difficult to resolve. It is notable that, in spite of the many viruses known to attack flowering plants, some of them capable of infecting many genera in both Monocotyledons and Dicotyledons, there is practically no knowledge of any affecting Cryptogams (excluding Bacteria). Whether this is due to lack of observation or whether they do not exist is not known.

The way in which many plant viruses are spread under natural conditions is still largely a mystery. Spread by contact between plants is unusual excepting in some of the most infectious and stable viruses, seed transmission is rare, occasional transmissions occur by natural grafts, and a large number, but by no means the greater majority of plant viruses, are known to be spread by insects, mainly belonging to the Hemiptera. Study of the relationships between insect and virus is greatly hindered by the feeding habits of the former and the difficulties of assessing the virus content of the insects, but much information bearing on this point has been gathered by most painstaking research. The author in summing up the evidence concludes that there is little ground for the belief that the viruses multiply in their insect vectors, which appear to act merely as a vehicle for the transfer of the former from diseased to healthy tissues. That this is so appears to be self-evident in many cases, as some viruses do not remain infective inside insects for more than a few hours, though others may persist for weeks.

The origin of viruses presents yet another problem, as several are known to have appeared in plants in a manner which is highly suggestive of spontaneous generation, and one case is discussed at considerable length in the chapter dealing with speculations on the origin and multiplication of viruses. This case is that of the paracrinkle virus affecting the King Edward VII potato and present in all tubers of that variety, which is said to have been raised from seed about the beginning of this century. It is unique in that it would appear to have no natural means of spread whatever and is never found in any other host, although it is easily transmitted by means of grafts to several Solanaceous plants. The discovery of the presence of nucleic acid in several viruses has been seized upon by more than one author as a means of deriving viruses from genes and other cell constituents which are supposed to have become malignant. While such speculation is stimulating it is based on very flimsy evidence, as Bawden is careful to point out.

Plant Viruses and Virus Diseases is a book which may be recommended to all interested in plant diseases and viruses in general. It is full of information and contains few mis-statements. A slight criticism that might be made is that the author's views of the unreliability of the physico-chemical methods used for determining the molecular weights and related properties of viruses are based on an incomplete understanding of the classical methods of Svedberg and his colleagues.

ROY MARKHAM

Soil and Plant Analysis. By C. S. PIPER. $8\frac{1}{2} \times 5\frac{1}{2}$ in. Pp. xiv + 368 with 19 figs. in the text. University of Adelaide, Adelaide. 1942. Price 15 *s*.

This monograph from the Waite Agricultural Research Institute has been prepared with a view to securing greater co-ordination in the methods used by Australian laboratories engaged in soil investigations, and follows an earlier publication having the same aims. It takes account of the experience and new conceptions accruing since 1928, the date of the original pamphlet, and is believed to cover a very wide range of soil conditions. It is prepared by a chemist of great experience in its field and comes from a laboratory where the methods described are in actual and frequent use; the author speaks of the valuable collaboration of his colleagues.

The methods described deal not only with the usual chemical determinations applied to soils, such as calcium carbonate, HCl-extract, organic content, etc., but also with the physical constants associated with the presence of water. Mechanical analysis, acidity and colour estimates are also treated. Biological fertility tests, of the Neubauer and Mitscherlich type are not discussed; but the Briggs and Schantz wilting point method is given in an appropriate place.

The first chapter deals with the collection of soil samples in the field and with their working-up in the laboratory. In each subsequent chapter the detailed directions for carrying out an analysis are preceded by a concise discussion of principles and concepts concerned. These are clear and lucid statements and should be of great value to those tackling a piece of work for the first time. In some instances a choice of methods is provided, especially where, in the author's opinion, it is valuable to have a rapid approximate method available as well as one capable of yielding results of a high order of accuracy.

Methods of estimating the metals appear under several headings, e.g. in the soil HCl-extract, under the heading of exchangeable cations ('exchangeable base') and in plant ash. Different methods of estimating potassium are given in each of these sections, but the reasons for the choice are not made clear. Similarly, since uniformity is desired, it is not evident why phosphorus is estimated in one section by a weighing method and in another by a colorimetric determination of phosphomolybdate blue. The colorimetric method recommended does not take advantage of the improvements introduced by Berenblum and Chain. It is pointed out that good results can be obtained by careful use of either of the two methods, the cobaltinitrate and the perchlorate, commonly employed for determining potassium. The usual objection made to the cobaltinitrite method, viz. that the potassium content of the precipitate varies with the amount of potassium present, is taken into account. It is claimed that the variation is consistent, and a correction table is provided for all titration values from 1 to 48 ml. The maximum correction is 4·35 %. Results for the metals in soils are consistently reduced to the form of mg.-equivalents per 100 g. soil, and convenient tables are provided for obtaining these from the analytical figures. It is considered preferable to express plant analyses as weights of the elements (not oxides) per 100 g. of oven-dried material; a conclusion with which it is easy to agree, except where it is desirable to reduce the results to mg.-equivalents, as in studies of the internal buffer systems.

The plant section deals only with the inorganic (ash) constituents, and careful consideration is given to the methods of ashing. It is pointed out that the weight of ash obtained varies with the method used, so that crude ash is not a value of much significance. The author goes so far as to suggest that the most reliable value for total ash is the sum of the individual constituents; but does not explain on what basis this 'sum' is to be obtained. It is made clear that a major difficulty in preparing an ash for analysis lies in the formation of intractable silicates, which, especially in determinations of trace elements, may introduce a large error. In the opinion of the author, a large part of the inorganic loss on ignition may commonly be due to this cause, however carefully the ashing is carried out. The advantages of the wet ashing method are fully brought out and a clear account is given of the simple precautions necessary to make the perchloric acid method safe. The few instances in which the wet ashing method is unsuitable; and the application of dry ashing in the presence of stabilizing agents, such as magnesium acetate, etc., are also described. A special section is provided for the treatment of the trace elements, boron, copper, cobalt, iron, manganese, molybdenum and zinc; together with the special precautions necessary for dealing with such small amounts. Preparation by wet ashing is particularly valuable here.

The publishers are to be heartily congratulated on the pleasant and practical get-up of this volume, and one cannot doubt that it will become a valued addition to the laboratory reference-shelf of many soil and plant analysts.

W. O. JAMES

Catalogue of the Vascular Plants of S. Tomé (with Principe and Annobon). By ARTHUR WALLIS EXELL. $10 \times 7\frac{1}{2}$ in. Pp. xi + 428, with 3 maps and 26 figures. London: Printed by order of the Trustees of the British Museum. 1944. Price 30s.

The islands of S. Tomé, Principe and Annobon lie in the Gulf of Guinea close to the equator; they are the continuation of the chain of volcanic peaks to which Cameroons Mountain on the African mainland and the island of Fernando Po also belong. All three islands are mountainous; S. Tomé, the largest of them, reaches a height of 2024 m. The climate is hot and moist; though the author describes it as 'typically equatorial', there is a fairly severe dry season, S. Tomé having two consecutive nearly rainless months.

Mr Exell's work, based on collections made during a visit in 1932–3 and on the results of earlier collectors, is the first complete flora of the islands and is a valuable contribution to knowledge of a phytogeographically very interesting area. All the Spermatophyta and Pteridophyta—native, introduced and cultivated—are enumerated and their synonymy and distribution inside and outside the islands are given. Descriptions (in Latin) are given only for new species and varieties (forty in number), but there are many useful critical notes. Appendices deal with non-vascular cryptogams collected by Mr Exell (among which it is interesting to note the British 'Lusitanian' moss, *Cyclodictyon laetevirens*) and with vernacular names.

The two introductory chapters give a concise but clear account of the geography and history of the islands and of the chief types of vegetation, as well as of the origin and affinities of the flora.

At the time of their discovery in 1470–1 the islands were uninhabited, but colonization soon took place and the cultivation of sugar-cane, coffee, cocoa and other crops has led to the destruction of a large part of the forests, which originally covered almost the whole land surface. Enough natural vegetation remains, however, to indicate the general nature of the original plant communities. In S. Tomé four 'regions' of vegetation are recognized: (i) the Littoral region, comprising a sand-dune and a mangrove formation; (ii) the Lower Rain Forest region from the coast to about 800 m., now mostly cultivated; (iii) the Mountain Rain Forest region from 800 to 1400 m., in which epiphytes are abundant and the fern flora richer perhaps than anywhere else in Africa; (iv) the Mist Forest region from 1400 m. to the highest summits. The mountain grassland, perhaps of biotic rather than climatic origin, which is found on Clarence Peak in Fernando Po and on Cameroons Mountain is not represented. The two smaller islands have similar, but less varied, vegetation.

The flora is similar to that of the neighbouring mainland, but includes some 171 species and two genera endemic to one or more of the islands. The absence of any native mammals except bats, as well as the nature of the flora, suggests that the islands have never been connected to each

other or to the mainland. A significant fact, which would give great satisfaction to Dr Willis, is that with a few exceptions, every species found on more than one of the islands also occurs on the mainland. A notable feature is the richness of the flora in orchids. The mountains are not high enough for a strong representation of temperate elements, and genera such as *Ranunculus* and *Geranium*, which are present on Fernando Po and Cameroons Mountain, are absent, but six species of temperate affinities occur on the mountains of S. Tomé.

The author, his collaborators, and the British Museum Trustees are to be congratulated on publishing such a valuable and excellently produced work in these difficult times.

P. W. RICHARDS

Flora of Egypt. Vol. I. *Pteridophyta, Gymnospermae and Angiospermae, part Monocotyledones: Typhaceae—Gramineae.* By V. and G. TÄCKHOLM in collaboration with MOHAMMED DRAR. $9\frac{1}{2} \times 6\frac{1}{2}$ in. Pp. 574. Bull. Faculty of Science, No. 17, Fouad I University, Cairo. 1941. Price 20s.

Work on this new *Flora of Egypt* was begun by Prof. Gunnar Täckholm and Mrs Täckholm in 1925, and after her husband's death in 1930 Mrs Täckholm has brought the work to completion herself. Throughout this task there has been close collaboration with Mr Mohammed Drar, who has given to the preparation of the flora his great experience of agricultural and applied botany, has been responsible for transliteration of all the Arabic names and citations, and has added a great number of new records and biological observations on the wild and cultivated plants of the country.

It is natural that a Flora of Egypt should be unique: so ancient a centre of civilization must necessarily bear the heavy stamp of human modification upon vegetation and flora; its traditional crops, weeds and introductions attract the interest which in other regions we find in the ecology of undisturbed natural communities. Quite rightly then, crops, weeds and introduced species are fully dealt with in the flora, and in this first volume, which includes Pteridophyta, Gymnosperms and part of the Monocotyledons, we find very extensive and informative treatment of the cereals now grown in Egypt.

There is, moreover, the prolific yield from the ancient tombs, of plant remains still in condition to be accurately identified. 'Egypt has what no other country possesses, a tomb flora. In this country every plant has a history. Owing to the dry and hot climate, nothing gets destroyed in Egypt.' Moreover, these discoveries may be set into a chronological scale unmatched for its accurate extension thousands of years back before the birth of Christ. Mrs Täckholm has taken advantage of these circumstances to the fullest degree, and has travelled to all the centres of learning where work has been done on the plants of the Egyptian tombs, especially to Berlin-Dahlem, where the great Schweinfurth's collection was housed, and whence she was able to procure his own unpublished manuscript notes on 200 identified species. The extensive literature has been searched and its content organized, so that we have a separate long section of the Flora dealing with each ancient plant of importance. In this way we have 'The Barley of Ancient Egypt' with separate accounts of the types found, citations of discoveries from Neolithic times onward through the dynasties of the Old, Middle and New Empires, Graeco-Roman and Coptic times, and reference to the work of Vavilov and Schieman on the possible origins of the cultivated plant. Similar full treatment is given in this volume to wheat and rice, but what is known of the ancient history of every single species is duly recorded. We cannot do better than quote from the opening pages a few striking instances of plant identifications and their consequences. Thus we learn of the import of *Taxus baccata* from Syria, of the extensive expeditions abroad for the trunks of *Cedrus libanoticus* for use as columns or flagstaffs in religious or ceremonial proceedings, of the employment of *Juniperus* berries in enbalming, of the prevalence of amber, and of the packing of a child mummy in dried *Zostera marina*, a plant apparently not native to the Egyptian coast. The publication of this collected material places upon archaeologist and botanist alike a heavy debt: to the one is given knowledge of economy, trade and custom, to the other knowledge of plant introduction, cultivation, utilization, and exact information of early range.

A third quality distinguishing the Egyptian flora from most others is the very renowned tradition of pharmacological botany founded upon it, and preserved not only in the writings of famous

arabic botanists, but in the living folklore of the Egyptian people. The authors have therefore followed the plan of giving full reference to all pharmacological employment of plants included in the *Flora*.

The three special and most commendable attributes of the *Flora* above-mentioned have apparently not jeopardized the normal and fundamental attributes of any flora. It is apparent that all the great herbaria of Egyptian plants have been worked over, that Mr Drar has contributed full knowledge of the living flora, and that specialists in the taxonomy of the difficult groups have very fully collaborated with Mrs Täckholm. A feature not so common in Floras as it should be, is the very copious reference to the scientific literature on all the manifold topics and fields of work considered.

It seems that having for many years felt acutely the need for an adequate Egyptian Flora, botanists will now have the satisfaction of working with one that is very good indeed. The Fouad I University Press, together with the authors, are to be congratulated on the production of this volume, and to be encouraged speedily to follow it with the others.

H. GODWIN

THE NEW PLANT GEOGRAPHY

An Introduction to Historical Plant Geography. By E. V. WULFF. Pp. xv + 223. Waltham, Mass.: the Chronica Botanica Company; London, W. 1: Wm. Dawson and Sons Ltd. 1943. \$4.75.

Foundations of Plant Geography. By STANLEY A. CAIN. Pp. xiv + 556. Harper and Brothers: New York and London. 1944. \$5.00.

These two books lead to the realization that a branch of botany which, though by no means new, has never been very prominent, has now emerged as an integrated study, wide in scope and very much alive. The difference in title, though intelligible and defensible, is nevertheless somewhat misleading. Dr Wulff divides plant geography into three sections: floristic, ecological and historical. The first is well represented in the work of Engler and Diels, and the second in Schimper's great book: both are primarily descriptive in method. There remains the analytical study of the distribution of species, floras and vegetation; the search for causal factors and their modes of operation. This is Dr Wulff's chosen field, and the present volume is a translation from Russian of the first of a series of three, the second of which, dealing with the History of the Floras of the World, was ready for publication at the outbreak of war. The third, dealing with the effect of man's activities, is in course of preparation. Prof. Cain also disclaims any intention of writing a descriptive plant geography, and he, too, is concerned with 'an interpretation of the phenomena of plant distribution'. But his treatment makes it clear that the epithet 'historical' gives somewhat too narrow an idea of a field of study in which experimental methods are beginning to play an important part, and suggests instead the term 'analytical plant geography'.

Dr Wulff's book has eleven chapters, of which the first two are introductory and historical. The next three deal with the various types of distribution areas, chapter VI with the parallelisms between the distributions of plants and animals and with the geographical relations between parasites and their hosts, chapters VII and VIII with the roles of artificial and natural factors in plant distribution, chapter IX with the migrations of species and floras, chapter X with the historical causes for present distributions, and the final chapter with floral 'elements'. The author is primarily concerned with the familiar old problems of geographical distribution, and he is easily recognized as the latest member of a long sequence of European writers on this subject, writers whose work he knows intimately and quotes repeatedly. He has produced a balanced and soundly critical statement of the problems and of the solutions which have been proposed for them. His examples are well selected and do not interrupt the flow of the exposition, so that the book is delightfully easy to read. English readers will find references to Russian work which is little known in this country, and will realize their debt to the Chronica Botanica Company for this widening of their horizons as well as for enabling them to benefit from Dr Wulff's authoritative judgement.

Prof. Cain's is a very different kind of book. Whilst the author reveals a close acquaintance with the older literature of the subject, he throws a strong emphasis on certain topics which have been

engaging the recent attention particularly of American plant geographers. The contrast is that between a writer in the main European tradition and one who is in intimate contact with the brilliant modern American schools of biological research. Of the five sections into which the book is divided the first is introductory, and only one of the remaining four, that on Areography, can be said to cover more or less identical ground with parts of Dr Wulff's book. The other three deal with Paleoecology, Evolution and Plant Geography, and the Significance of Polyploidy for Plant Geography respectively. The treatment is detailed, so that the book makes by no means light reading, though the main argument can easily be followed through the adoption of the valuable device of heading each chapter with a brief and well-worded summary of its conclusions. But Prof. Cain is much to be thanked and congratulated for bringing into one convenient volume so much that is absorbingly and excitingly interesting.

The feature of Dr Wulff's book which is likely to leave the deepest impression is his steady development of the view that the 'structure of the areas of species and the composition of floras cannot be explained by existing factors', and the consequent soberly enthusiastic support of Wegener's theory of continental drift as providing the best available explanation of many of the original problems of plant geography. As Seward has stated 'the Wegener hypothesis appeals strongly to the imagination', and this makes it the more important that the botanical evidence should be assessed with the greatest possible objectivity. Dr Wulff is at pains to present the arguments of both sides, and his analysis shows that the case for Wegener is a strong one, although outstanding difficulties over Pacific floras demand some modification of the original form of the hypothesis.

The accounts of the geographical relationships of parasites and their hosts, and of the disharmonies between the life histories and present environments of certain plant species, based largely on Russian work, provide interesting evidence of past migrations induced by climatic change. Of our native British plants, *Hedera helix* and *Colchicum autumnale* are cited as examples of disharmonious periodicity: *Lamium album* might have been added to the list. *Calluna* is regarded as retaining an ancestral 'xerophytism' that originated under conditions different from those now prevailing over the greater part of its area. Here the translator may have done Dr Wulff an injustice, but that there is a problem is clear enough, and it is to be hoped that we may soon learn something of the Tertiary distribution of heather.

Dr Wulff deals rather sketchily with the mechanism of speciation, and accepts the view, perhaps too readily, that 'extreme climatic or other habitat conditions induce doubling of the chromosome number'. But he shows his scientific judgement to great advantage in his treatment of the various kinds of endemics and in the chapter on floral elements. In both cases he resists the temptation to make a single neat classification of the observed phenomena, and reveals their real complexity. It is his balanced objectivity that gives his book its great value.

After a very concise statement of general principles Prof. Cain gives the best available account of the methods and findings of the American 'paleoecologists'. It is a most impressive story of the reconstruction through painstaking research of the history of plant communities from early Tertiary times to the present day. Chaney's work on the redwood forest is described in some detail, and provides a fine example of the fruitfulness of the new techniques of interpretation. This magnificent community has been traced from its Eocene centre in Alaska through the various stages of its southward migration and floristic impoverishment in later Tertiary times to its relict condition to-day. Accounts are also given of the history of the closed-cone pine forests, now confined to California, and of the desert climax, the work chiefly of Mason and Clements respectively. A chapter on pollen analysis gives a critical assessment of the method and is further valuable to English readers in summarizing American evidence for the climatic 'revertence' first established from European diagrams. It is interesting to read that the Arctic timber line in Alaska is advancing, while that in eastern North America is retreating. Prof. Cain infers that 'Shifts of climate such as apparently are now taking place...do not invalidate the principle of regional parallelism in pollen analysis but do make more difficult the problems of synchronism'.

It is impossible in a short review to do full justice to the rest of Prof. Cain's book. The 720 references in his bibliography give some idea of the thoroughness with which he covers his field and of the value of the book merely as a compilation. But it is much more than that. The discussion of the interpretation of the various types of distribution-areas is critical and masterly. A whole chapter is devoted to an examination of the concept of species senescence, and the conclusion is reached that the view that certain species are physiologically old or young is not soundly based. In contrast with Dr Wulff he devotes a whole section of five chapters to the significance of polyploidy for plant geography, and summarizes the vast American contribution to this topic. As the

section on paleoecology emphasized the importance of ecological concepts and methods, so this makes it clear that the plant geographer must work in close touch with the cytogeneticists also. The growing unification of botany, and indeed of biology, is brought home to the reader of this book with overwhelming force.

Amongst the general impressions left after reading these two books is that west European botanists must accept the challenge to reconstruct the history of their plant communities through Tertiary times. We know a great deal about forest history in post-glacial times and in some of the inter-glacial periods, thanks especially to the peat analysts, but much more must be done, and with improved methods, before we can write such a story as that of the redwood forest in west America.

Neither book deals adequately with the problems of the effect of soil development, apart from climatic change, on plant communities. The vegetational differences between the new drifts in eastern and the old drifts in western Schleswig-Holstein emphasize the importance of this point. There must have taken place far-reaching floristic changes *pari passu* with the leaching of the older drifts. Can the record of these changes be disentangled from the effects of climatic change?

While both authors conclude, very rightly it would seem, that 'plant dispersal in most cases is not saltatory....Plants extend their range slowly, gradually, step by step', there still remains the obstinate problem of the meaning of 'in most cases'. How did *Vaccinium vitis-idaea* and *V. uligi-nosum* reach the dune-heaths of the Dutch island of Vlieland: and how did *Cornus suecica* reach its west Yorkshire locality? Are they relics or bird-carried 'pseudo-relics'? The long-continued close observation of well-selected small areas may some day bring us nearer to a solution of this problem. And finally, there must always be borne in mind Polunin's warning that discontinuous distributions of easily overlooked species may be only apparently discontinuous.

In conclusion it should be added that both books have had, unfortunately, to be printed on war-time paper, and that some of the maps in Dr Wulff's book are quite inadequately reproduced. Misprints occur in both, but are for the most part unobtrusive and unimportant.

A. R. CLAPHAM

SOCIETY FOR EXPERIMENTAL BIOLOGY

The fifty-ninth Conference was held at the London School of Hygiene on 2–4 January 1945.

A symposium on Soil Metabolism was held under the Chairmanship of Prof. Salisbury. All the papers were by members of the Agricultural Research Council Soil Metabolism Unit under Dr Quastel's general direction and he introduced the symposium, referring in particular to the manometric and perfusion techniques used to study nitrogen and manganese metabolism in soils.

Dr Lees, who described the perfusion technique in some detail, showed how it could be used to study oxidation of ammonium to nitrate in soil. The results proved that the oxidation is mainly biological and it proceeds on soil crumb surfaces at the expense of ammonium ions adsorbed in the base-exchange complex of the soil. Addition of millimolar chlorate to soils nitrifying ammonium causes accumulation of nitrite instead of nitrate, and this has been shown to be due to the inhibitory effects of chlorate on the growth of nitrite organisms. This effect is antagonized by nitrate ions. It suggests that the normal accumulation of nitrate in soil proceeds via nitrite.

Dr Dion dealt with the forms in which manganese occurs in soils; his work showed that considerable amounts of manganese are extracted from soils by orthophosphate solutions in the form of a complex anion, mangani-di-orthophosphate. This manganese is in the trivalent state, and there is good evidence that divalent manganese added to a neutral soil undergoes oxidation largely to the trivalent state which undergoes further changes to give MnO_2.

Dr Mann described the manometric technique devised for determinations of MnO_2. Oxidation of hydroxylamine by MnO_2 in acid solution yields nitrous oxide. The technique has been used to study oxidation of manganous salts added to soil in the perfusion apparatus. This oxidation is inhibited by chloretone, sodium azide and iodacetate; also by heat sterilization. There is little doubt that in the soils studied manganese oxidation is brought about by biological means. Reduction of MnO_2 to the manganous ion by biological agencies can occur under certain conditions.

Dr Webley described a technique for evaluating oxygen availability to soil bacteria. The method consists in spreading a suitable test organism together with organic substrate over the soil and determining oxygen uptake manometrically.

A symposium on the Structure of Viruses was held under the Chairmanship of Dr R. N. Salaman. It was introduced by Dr F. C. Bawden, who referred to the introduction of the techniques of protein chemistry in the study of plant viruses. Such technique had shown that some viruses at least differ fundamentally from bacteria and other organisms. A dozen or so viruses have been isolated in apparently pure states as nucleoproteins; all have contained a ribose nucleic acid. The ratio of nucleic acid to protein is different in different viruses, and the two components may be combined in different ways, for they are easily separated with some viruses but not with others.

Particle shape is responsible for some of the most striking differences between purified preparations of different viruses. Solutions of those with spherical particles, such as tomato bushy stunt and tobacco necrosis viruses, have normal physical properties, and by appropriate treatment these crystallize in forms characteristic of the individual virus. Solutions of those with elongated particles, such as tobacco mosaic virus and potato virus X, are anomalous in all their physical properties; these form liquid crystals. It is suggested that the greatly elongated particles do not occur in the plant but are produced during purification by the linear aggregation of small particles. This may occur when materials combined with the viruses are removed, and the purified nucleoproteins should be regarded merely as the simplest chemical forms of the viruses.

Dr W. T. Astbury dealt with 'Structure of viruses and nucleoproteins'. Present indications are that viruses are essentially of a nucleoprotein nature, and that their activities are an aspect of the nucleoprotein metabolism that seems to be the ultimate molecular basis of all the phenomena of reproduction and growth. Nothing precise is known yet about their architecture, but definite progress is now being made with regard to the two components, protein and nucleic acid. The fundamental relationship between the two suggested by X-ray studies is that the nucleic acids consist of columns of flat nucleotides whose distance apart (3·34 A.) is exactly equal to the distance between successive side-chains in an extended polypeptide. From this dimensional correspondence must arise a reciprocal 'template' action that ensures transmission of the indispensable molecular patterns.

It is remarkable how in the tobacco mosaic virus, for instance, a single nucleotide serves in effect to co-ordinate some fifty-four amino-acid residues. Cohen and Stanley have now made un-depolymerized preparations of the nucleic acid from this virus, and find an initial molecular weight of about 300,000. From the X-ray data this would correspond to the observed unit length of the virus particle (about 2800 A.), suggesting that the acid lies in columns along the length of the particle, either on or near its surface.

Dr F. M. L. Sheffield described the R.C.A. electron microscope and methods of preparing biological specimens for examination with this instrument, touching on some of the difficulties encountered. Electron micrographs of purified virus preparations confirm many deductions made by indirect methods of the sizes and shapes of plant viruses. It was generally agreed that tobacco mosaic virus has rod-shaped particles 15 mμ wide, but there was much controversy about the length which micrographs show to vary. It is now deduced, and confirmed by micrographs, that the length of the rods vary according to the method of preparation. Potato virus X is also rod-shaped whilst the particles of bushy stunt virus and tobacco necrosis virus are spheres with a diameter about 35 mμ.

Some viruses which have shapes readily distinguishing them from other plant constituents can be identified by the electron microscope in the crude plant sap. (Examples shown were tobacco mosaic virus and potato virus X.) It is thus a possibility that some of those economically important viruses which cannot be isolated may be studied in this way.

Viscosities of tobacco mosaic virus solutions were discussed by Dr R. Markham. Theory predicts that the viscosity increment of rod-shaped particles should increase as the square of their length if measured at sufficiently low velocity gradients, and thus viscosity measurements afford a simple and sensitive test of changes in the length of the virus rods. It is difficult, however, to interpret these results in terms of the length of the molecules, as solutions are almost invariably polydisperse, and it is possible to increase or decrease the viscosity of the solutions by simple physical manipulations as well as by chemical treatments. The use of the co-axial viscometer eliminates most of the troubles occasioned by flow in a capillary viscometer, and it can be shown that at low velocity gradients the viscosity increment of the virus solutions reaches a maximum value. There is therefore little justification for the statement, based upon measurements with a capillary instrument, that viscosity measurements at negligible shear may be combined with sedimentation and diffusion measurements to give entirely conflicting results.

In view of the difficulty of interpreting the data quantitatively it is concluded that viscosity measurements may best be employed in a qualitative manner for detecting changes due to various treatments.

Dr Lea discussed joint work with R. Markham, M. H. Salaman and K. M. Smith on inactivation of viruses by radioactive and X-radiations. Such radiations cause ionization of atoms, and any molecule of which such an ionized atom is part usually suffers chemical change. The molecular weight of a substance can be determined roughly by measuring the dose of radiation needed to decompose it. The assumption involved is that a single molecule is decomposed by a single ionization. The method has yielded fair results with enzymes.

Applied to small spherical plant viruses and bacteriophages the method gives estimates in fair agreement with the accepted size. Applied to rod-shaped viruses the method gives sizes smaller than the size of the whole rod which may indicate that the molecule is smaller than the rod. The method may be used to distinguish between a virus which is a macromolecule and one more of the nature of a unicellular organism. Plant viruses and the small phages behave as macromolecules, while the behaviour of vaccinia is not that of a macromolecule.

Serological studies on plant viruses were dealt with by Dr Kleczkowski who discussed principally the precipitin test.

In quantitative serological studies with purified preparations of tobacco mosaic and tomato bushy stunt viruses antibody/antigen ratios in precipitates formed at optimal combining proportions were found to be respectively 0·2 and 0·4. These values are intermediate between those for precipitation of small particle antigens, e.g. ovalbumin or serum proteins, and for agglutination of large particle antigens, e.g. bacterial suspensions. This is a reflexion of the fact that the size of virus particles occupies a similarly intermediate position.

The character of the precipitate formed by a plant virus with its specific antiserum is determined by the shape of the virus particles. Viruses with long rod-shaped particles form precipitates resembling in all respects flagellar or 'H'-type bacterial agglutination, whereas viruses with spherical, or almost spherical, particles form precipitates resembling somatic or 'O'-type bacterial agglutination.

Certain plant viruses can form complexes with some other unspecific proteins. Such complexes can combine with virus antibodies and give a positive complement-fixation test, though they are often unable to precipitate with them. These complexes can be split by proteolytic enzymes, and the virus released in a form precipitable with virus antiserum.

Prof. Gregory took the Chair at a session of papers chiefly devoted to seed or seedling metabolism. Miss M. M. Edwards described work on germination of seeds of *Striga lutea* which normally only germinates when in contact or very close to roots of the host plant. This was shown to be due to a substance diffusing from the host roots. Methods of isolation were described, and the substance (whose chemical nature is under examination in the Department of Chemistry in Manchester) was shown to be very readily destroyed by oxidation by air. Influence of various pre-treatments of seed on germination induced by this substance were considerable. Artificial dormancy breaking substances have some effect on germination of *Striga*.

Dr R. Brown dealt with aspects of protein metabolism of embryos excised at very early stages during growth of germinating barley grain.

Mr Oxley described investigations on the respiration of wheat grains. The respiration rate increases irreversibly with time, but there is no corresponding increase in the size or differentiation of the embryo. From this, and the observation that grains from which the embryos had been removed respired as rapidly as whole grains, it was concluded that the main seat of respiration is external to the embryo. Experiments were described in which much of the 'bran' of grains was removed by abrasion without impairing germinative capacity. The respiration rate was reduced by this treatment to between 5 and 50 % of its original value. It was concluded that the main seat of respiration is in the bran, but, since most of the tissues of this structure appear to be dead, it was ascribed to micro-organisms presumably resident within or upon the bran. Investigation showed that normal wheat grains have a fungal mycelium developed below the epidermis of the pericarp, but, unless the grain is obviously mouldy, there is no sign of micro-organisms other than spores on the outer surface. The apparent respiration of wheat grains too dry for germination is ascribed largely to this mycelium.

NOTICE

As increasing means of communication become available with different parts of liberated Europe botanists will wish to re-establish those contacts with scientific colleagues broken during the war years. To facilitate this the editors of the *New Phytologist* propose to print a list of names and addresses of botanists whose whereabouts in the liberated countries have been ascertained. The editors will be glad to receive information on which to base such a list.

STUDIES IN THE DEPTH ADJUSTMENT OF SUBTERRANEAN PLANT ORGANS

I. RAUNKIAER'S EXPERIMENT ON DEPTH PERCEPTION IN *POLYGONATUM*

By A. R. CLAPHAM

University Department of Botany, Sheffield

(With 1 figure in the text)

Species of *Polygonatum* have long been known to have rhizomes which adjust themselves to a 'normal' depth below the soil surface through a capacity to curve upwards or downwards when displaced. No satisfactory explanation of this behaviour has so far been proposed, but Raunkiaer (1907; translated into English in Raunkiaer, 1934) carried out an experiment which led him to the view that the rhizome 'perceives' its depth below the soil surface through the darkening of a greater or smaller length of the basal part of the erect shoot. He planted a rhizome 5 cm. below the soil surface in a pot, and caused the aerial shoot to grow up through a cardboard cylinder 10 cm. high, covered at the upper end. When the shoot reached the top it was allowed to emerge through a perforated cork, the hole being packed with wadding wool so as still to exclude light from the part of the shoot inside the cylinder. 'When the plants were taken up in the following August...in the plants whose aerial shoots had not grown up through the cylinder the new segment of rhizome had grown approximately horizontally or slightly downwards; in the individuals whose aerial shoots had grown up through the cylinder and had not come into contact with light till reaching its edge, the new portion of the rhizome was directed obliquely upwards.... From this it follows that the plant really determines its depth by means of the epigeal portion of the shoot, and that it measures the depth by the distance from the rhizome to the place where the epigeal portion of the shoot reaches the light; this distance will, of course, coincide in nature with its real depth' (Raunkiaer, 1934, pp. 73–4).

The result of this experiment and the conclusion drawn from it are of very great interest, and it seemed desirable that a more detailed investigation should be made, both in order to confirm the reported facts and to explore the mechanisms of perception, transmission and response.

Plants of *Polygonatum multiflorum* (Moench) L. from the Oxford Botanic Garden were lifted in May 1944, when their aerial shoots were already 15–35 cm. above the ground. They were grown in large cylindrical glazed pots 25 cm. in diameter and 25 cm. deep (internal dimensions) and with basal drainage vents. Rhizomes selected for straightness were planted horizontally in good garden soil at known depths below the surface. Three or four rhizomes were planted in each pot, all at the same depth. The range of depths in different pots was from $\frac{1}{2}$ in. (1·25 cm.) to 8 in. (20 cm.) below the soil surface. In each pot at least one plant had its aerial stem darkened for part of its length below the lowest leaf, and at least one was untreated. Darkening was effected sometimes with

narrow cardboard cylinders but more usually with glass tubing, $c.$ $\frac{1}{2}$ in. in diameter, covered with thick black paper, the lower end buried in the soil and the upper end packed with cotton wool round the emerging aerial shoot. When other than basal parts of the aerial shoot were darkened, the cardboard cylinders or glass tubes were packed both above and below with cotton wool. In all cases the cotton wool was held in position with cellophane, and the cylinder or tube was supported by tying to a cane driven into the soil. Most of the pots were placed on the open roof of the Oxford Department of Botany, but one pot with three rhizomes at $\frac{1}{2}$ in. below the soil surface was placed in a dark room. Finally several small rhizomes were placed on the surface of the soil in a pot which stood in a sink in the Department of Botany. All the pots were watered from above when necessary. The aerial shoots developed normally and flowered, except those in the dark room which died after about 3 weeks.

The plants were lifted on 12 September 1944, when the new segments of rhizome had completed their growth. It was then found that results comparable with those of Raunkiaer had been obtained in some of the experiments. For instance, pots D and E, with rhizomes at $\frac{1}{2}$ in. depth, each showed one plant (D1 and E1) with aerial shoot not darkened whose new rhizome segment had grown steeply downwards; and one plant (D2 and E2), with a basal length of 8 in. in E2 and 14 in. in D2 darkened as described above, whose new segment had grown horizontally (Fig. 1, c, d of plants D1 and D2). Other pots, however, gave conflicting results. Thus in pot C, whose rhizomes were also at $\frac{1}{2}$ in. depth, a plant C1 with aerial shoot untreated, and another, C2, with an unblackened glass tube round the basal 6 in. of its shoot, had new rhizome segments growing horizontally, while the third plant, C3, with the basal 7 in. of its aerial shoot darkened, showed a steeply descending segment (Fig. 1, e, f of plants C2 and C3). Similarly in pot A, with rhizomes at 3 in. below the surface, the control plant A1 had a horizontally growing segment, while the plant A3 with the basal 7 in. of its aerial shoot darkened had a descending new segment (Fig. 1, g, h). There was no consistent effect of darkening either the basal part or any higher part of the aerial shoot.

The two rhizomes at 5 in. depth, one with aerial shoot darkened at its base, both grew more or less horizontally (Fig. 1 i), and the two at 8 in. depth both grew obliquely upwards (Fig. 1 l). The three rhizomes at $\frac{1}{2}$ in. depth in the dark room grew steeply upwards (Fig. 1 m–o), and those planted on the surface in the light grew steeply downwards (Fig. 1 a, b).

These last two results suggest that rhizomes of *Polygonatum* behave like those of many other rhizomatous plants in reacting to light by developing strong downward or dorso-convex curvatures (Raunkiaer, 1934, pp. 92–4). Similar curvatures in the plagiotropic stolons of *Ajuga reptans*, *Ranunculus repens*, *Hieracium pilosella*, etc., have been shown by Maige (1900), Zimmermann (1924) and others to be epinastic or positive geotropic and not negative phototropic curvatures. In these plants, too, the stolons grow vertically upwards in the dark (Czapek, 1895; Maige, 1900).

The rhizomes exposed to light on the surface of the soil were seen to develop both chlorophyll and a deep purple anthocyanin. Closer examination of the rhizomes planted below the surface then revealed that all those which showed a similar pigmentation also showed a downward growth of the new rhizome segment. Thus plants D1, E1, C3 and A3 all showed a considerable development of pigment, while the other plants in the same pots, whose rhizome segments grew horizontally, showed no pigment. No
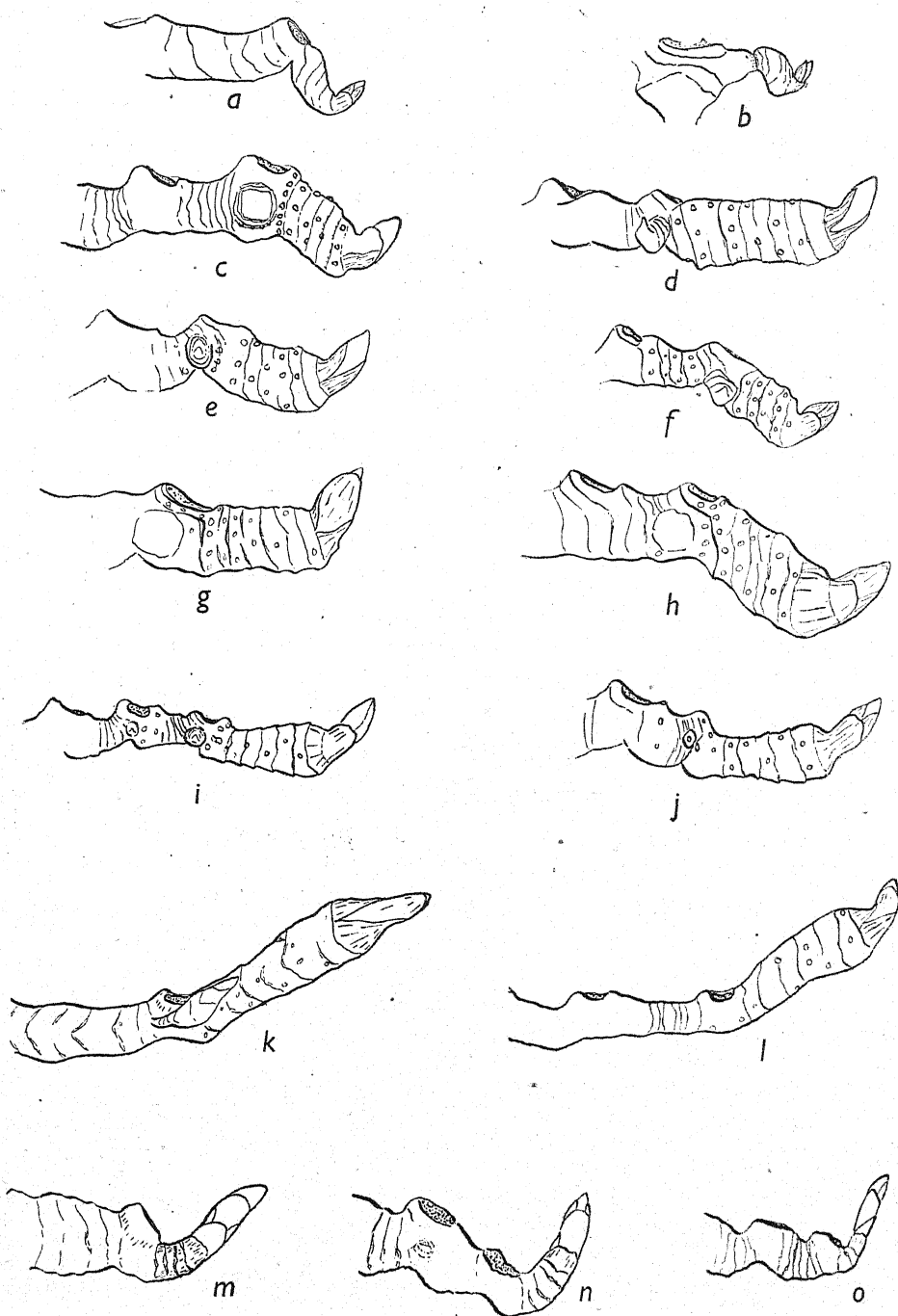
Fig. 1. *a, b*: rhizomes planted on the soil surface, fully exposed to light (*b* shows a new rhizome segment from a lateral bud on a fragment which had no aerial shoot in the current season). *c, d*: plants D1 and D2 respectively, at ½ in. depth. In *c* the erect shoot was exposed to light, but in *d* its basal 8 in. were darkened with a cardboard cylinder. *e, f*: plants C2 and C3 respectively, at ½ in. depth. In *e* the basal 6 in. of the erect shoot were enclosed in an unblackened glass cylinder; in *f* the basal 7 in. were darkened. *g, h*: plants A1 and A2 respectively, at 3 in. depth. In *g* the erect shoot was exposed; in *h* the basal 7 in. were darkened. *i, j*: planted at 5 in. depth. In *i* the erect shoot was exposed; in *j* the basal 3 in. were darkened. *k, l*: planted at 8 in. depth. In both the erect shoots were exposed. *m, n, o*: planted at ½ in. depth in the dark room.

8-2

rhizome at 5 in. or at 8 in. depth showed pigmentation, nor did those in the dark room.

It appears then that the experimental conditions made it possible for light to reach rhizomes planted 3 in. below the surface. In some cases it was obvious that watering the pots from above had caused a small annular hollow to develop round the base of some of the aerial shoots, and round the glass tubes which were used to darken the basal parts of stems; and it seems certain that this enabled light to penetrate in sufficient intensity to cause pigmentation, especially since pigmentation was often confined to an area round the base of the aerial shoot, and was never absent from this region in rhizomes with more widespread pigmentation.

If it be supposed that the direction of growth of the new rhizome segment is determined by the intensity or quantity of light reaching either some part of the rhizome itself or some sensitive region at the base of the erect shoot, but not by the length of the darkened portion of the erect shoot, all the results of the experiments with rhizomes planted at depths not exceeding 3 in. are readily explicable. For the direction of growth may then be regarded as the result of a balance between the negative geotropism shown in darkness and the light-induced dorso-convex curvatures shown by exposed rhizomes, the strength of the latter being dependent on light intensity. It still remains, however, to account for the difference in behaviour between the rhizome in Raunkiaer's experiment which grew obliquely upwards when planted at 5 cm. depth with its shoot growing through a cardboard cylinder, and those in the present experiments which grew more or less horizontally at depths down to 5 in. (12·5 cm.), although not perceptibly pigmented. There are two obvious differences in the experimental conditions. The aerial shoot of Raunkiaer's plant grew upwards in the dark until it reached the top of the cardboard cylinder, whereas in the present experiments plants were used whose shoots had already emerged into light at the 'normal' height above the rhizome. This can hardly explain the difference in question, since the whole range of rhizome behaviour was found in the present experiments, and variations in behaviour clearly depend on variations in subsequent conditions, presumably in those operating when the new rhizome segment is beginning its growth. The second difference is that Raunkiaer darkened the aerial shoot with a very wide cylinder (Raunkiaer, 1934, fig. 47, p. 74), which would incidentally darken the soil surface over much of the length of the rhizome, while in our experiments the much narrower tubes darkened a correspondingly smaller area of the surface. It is tempting to infer that the observed differences are related to differences in light intensity at the sensitive part of the rhizome or shoot base. This would mean that in our experiments sufficient light must have penetrated, even to a depth of 5 in., to cause a tendency to dorso-convex curvature balancing the negative geotropism of the rhizome, but that this light was insufficient to cause pigmentation, and would imply also that under natural conditions depth adjustment is at least partly determined by light penetrating down to the sensitive region.

In order to investigate light penetration into soil small squares of fast bromide paper (2 × 2 cm.) were placed in cellophane envelopes stiffened with cardboard on the lower side. They were then buried at various depths in pots of dry soil and left for 3 days exposed to the light of a 60 W. lamp at 22 cm. above the soil surface. The soil was from the bottom of Totley Wood near Sheffield, and had a good crumb structure. It was used in the air-dry condition to protect the cellophane and bromide paper from damage

by moisture. The bromide papers were buried, two at each depth, at $\frac{1}{2}$, 1, 2, 3, and 5 in. below the soil surface, and two controls, handled in precisely the same way, were kept in a dark room in the original envelope. The first experiment showed considerable light penetration to $\frac{1}{2}$ in. and slight penetration to 1 in. Another set of bromide papers were then left for 7 days, the soil surface being illuminated with a 100 W. lamp at 22 cm. The results were much as in the first experiment, but with a very slight darkening of one of the two bromide papers at 2 in. depth.

The conclusions to be drawn from these observations must be that light may penetrate to considerable depths through undisturbed loose soil, and will reach still greater depths down the cracks which form in many soils when they become dry or down the annular hollows made by percolating water round the bases of aerial shoots or any other objects which break the soil surface. If the rhizomes of *Polygonatum* may be supposed sensitive to light of very low intensity, an explanation is afforded of the failure of those at depths as great as 5 in. to rise as did those at 8 in. and in complete darkness in our experiments, and as did the one beneath a wide cardboard cylinder in Raunkiaer's experiment. Observations are clearly required on the reactions of the rhizomes in light of known intensities.

The location of the pigment in rhizomes which showed a downward growth suggests that the sensitive region, if actually situated on the rhizome, must be close to the base of the erect shoot. It may lie on the old rhizome segment of last season, or more probably may be the apical region of the new segment. That it is unlikely to involve the base of the erect shoot of the current season is suggested by the downward growth of segments from lateral buds on severed portions of rhizome, with no erect shoot of the current season, which were planted on the surface of the soil in the light (Fig. 1 *b*). Here again further observations are required.

SUMMARY

An attempt was made to repeat Raunkiaer's well-known experiment on depth perception by the rhizome of *Polygonatum multiflorum*. The results lead to a reinterpretation of Raunkiaer's experiment, since the factor determining the direction of growth of the new rhizome segment appears to be the intensity of light reaching some part of the rhizome, rather than the length of the darkened part of the erect shoot.

The direction of growth appears to be the result of a balance between negative geotropism and a tendency to dorso-convex curvature whose strength depends on the intensity of light reaching the sensitive region of the rhizome. This region may lie close to the base of the erect shoot, but its exact position has not been determined.

It is shown that light can penetrate to considerable depths in loose soil.

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PLAGIOTROPISM AND CORRELATIVE INHIBITION

By R. SNOW
Fellow of Magdalen College, Oxford

(With 1 figure in the text)

It has long been known that in various Abietineae the leading shoot exerts an influence which depresses the lateral branches to their normal angle of orientation. It does this by inducing in them an 'epinastism'—that is to say, a tendency to epinasty—which opposes their negative geotropism (see Münch, 1938, p. 645 seq. and p. 650 seq.). Similarly in many flowering plants the apical bud induces epinastism in the lateral shoots. The question therefore arises how this induction of epinastism is related to the correlative inhibition which is brought about by the main shoot apex in the lateral buds and shoots of many other species of flowering plants and also in some of the lateral buds and shoots of the same species of Abietineae, as Münch (1938, p. 643) has shown.

This question, amongst many others, has been discussed by Münch (1938) in the course of a very full and valuable paper dealing with the ways in which the growth and orientation of the shoots are regulated in trees, especially in Abietineae. He concludes (p. 667) that the prevention by the leading shoot of the geotropic erection of the lateral branches is equivalent to ('gleichbedeutend mit') correlative inhibition, and this conclusion may perhaps be understood in the sense that the two effects are alternative reactions to the same transmitted influence. This conclusion gains support from some preliminary experiments in which Münch (1938, p. 666) cut off the apical buds of various plants and applied a paste of hetero-auxin to one side of the stump. In one of the species tested, *Eupatorium cannabinum*, the top lateral shoot of the auxinated side was found to be a little curved by epinasty, besides being a little retarded in growth, whereas the opposite lateral was erect. Since therefore hetero-auxin applied to a decapitated stump in place of the apical bud can apparently induce epinastism in a lateral and can also inhibit a lateral, both in the same species and also, as is well known, in other species generally, it follows that the first stage in the processes leading to epinastism and to inhibition is the same.

However, the writer (1937, 1938) has brought forward evidence which he believes to show that correlative inhibition is not caused directly by the auxin in the main stem, and indeed that this auxin scarcely enters the inhibited laterals appreciably. Münch (1938, p. 642) accepts this evidence as convincing, and he appears to favour the writer's further conclusion that the inhibition is due to some secondary substance or process which originates from an earlier process started by the auxin descending the main stem and travels up into the laterals. So if this is so, the later stages in the transmission of the influences leading to inhibition and to epinastism may still be different; and consequently it is possible that inhibition and epinasty may after all not be equivalent in the sense of being alternative reactions to the same transmitted influence, but may instead be reactions to two different influences transmitted simultaneously. Accordingly the writer has per-

formed a few experiments, which will here be reported, to test further the idea that correlative inhibition and epinastism are equivalent.

To find a good plant for experiments on the induction of epinastism by the apex is not entirely easy, for the woody conifer branches react only slowly and in many flowering species the lateral shoots are more or less permanently epinastic, and do not curve up when the apical bud is removed, or only very slowly. But the big, vigorous annual *Impatiens Roylei* (Walp.) was found very good, its only disadvantage being that when it was grown in pots, its lateral shoots did not develop well and reacted quite erratically, probably because the strong root system quickly became pot-bound, so that only experiments on plants in the ground were of any use. The mature leaves are grouped in secondary whorls of two, three, or four, and the lateral buds in their axils grow out at an oblique upward angle of about 45°. When the laterals are 3 or 4 cm. long they begin to make epinastic curves which depress them about to the horizontal or even a little below it, though their curves do not reach quite to the tips, which still point obliquely upwards (see Fig. 1, *c*). If the apical part of the main shoot is removed, some of the upper remaining laterals curve upwards instead and soon reach the vertical.

In one pair of seedlings of *Impatiens Roylei* the main shoots were decapitated in May by cuts below the developing leaves, and only the axillaries of the cotyledons and of the lowest whorl of leaves, which were about 1·5 and 1·0 cm. long, were allowed to remain. One of the seedlings was given a cap of lanoline containing hetero-auxin at 1 in 350, which was applied all over the top of the stump of the main stem, not on one side only as in Münch's experiment. The hetero-auxin crystals were old, and had only about one-third of the full strength.

After 16 days the axillaries of the cotyledons had grown in both plants equally, to about 6 cm., but in the plant with hetero-auxin they pointed upwards (apart from their extreme tips) at angles of only 30 and 25° and were curved dorso-convex, whereas in the plant without hetero-auxin they pointed 65° upwards and were curved slightly dorso-concave.

The axillaries of the lowest leaf whorl, which grew out rather later, reacted similarly. After 20 days they had grown to about 4·5 cm. in both plants, but in the plant with hetero-auxin they pointed upwards at only 30 and 10° and were curved dorso-convex, whereas in the plant without hetero-auxin they pointed up at 50° and were curved dorso-concave.

Another pair of plants was treated similarly when the axillaries of the cotyledons were only about 0·75 cm. long. They reacted similarly; for after 13 days in the plant with hetero-auxin paste these axillaries had grown to 4·5 and 4·0 cm., pointed only 20° upwards and 0° (horizontally) and were curved dorso-convex, whereas in the plant without hetero-auxin at 16 days they had grown to the same length (4·5 cm.), but pointed 70 and 60° upwards and were curved dorso-concave.

So these results confirm Münch's result; for the hetero-auxin paste, applied in place of the apical bud, made the laterals epinastic and so prevented them from curving up by geotropism: it did not retard their growth.

Since therefore it may be concluded that the first stage in the correlative induction of epinastism in laterals depends on the auxin secreted by the main apical bud, just as does in other species the correlative inhibition of orthotropic laterals, it is of interest to determine how this process will be affected if the lateral shoot is deprived of its developing leaves. For if in other species, such as peas or broad beans, plants are prepared

with two equal orthotropic shoots growing in balance, and if one of the shoots is deprived
of its developing leaves or is darkened, which treatments both diminish greatly the
formation of auxin, then the shoot so treated is quickly inhibited by the other one, as
the writer has shown (1931). So what will happen if a plagiotropic lateral is treated
similarly?

It was found that in *Impatiens Roylei* the lateral shoots deprived of their developing
leaves *rose* considerably by curving dorso-concave and were also strongly retarded in
growth, whereas similar intact laterals grew on well and remained straight or dorso-
convex provided that the light came from all round so that phototropism did not interfere.

Two examples will be given. In one young *Impatiens* plant one out of three similar
shoots in the axils of a whorl of mature leaves was deprived of its developing leaves
including those only 1 or 2 mm. long. The three lateral shoots were about 5·5 cm. long
and pointed about 30° upwards. The main shoot was of course left intact.

After 9 days the defoliated lateral had risen 35° by curving dorso-concave and had
grown only 1·0 cm. The two intact laterals were still straight, and one had not risen,
while the other had risen only 10°; but they had grown about 6 cm.

In another *Impatiens* plant one lateral shoot (*a*) out of three in the axils of the lowest
whorl of leaves was deprived of its developing leaves and was also decapitated by a cut
very close behind the stem apex and capped with vaseline. Another lateral (*b*) was treated
similarly except that it was capped with 1 in 350 hetero-auxin paste, and the third lateral
(*c*) was left intact. The three laterals were about 4 cm. long and all were dorso-convex.

After 14 days lateral (*a*) (with vaseline) had curved dorso-concave and had risen 20°,
while lateral (*b*) (with hetero-auxin paste) and lateral (*c*) (intact) were both dorso-convex
and had both sunk 20°. Lateral '*a*' and also lateral '*b*' had grown only 1 or 2 cm., while
'*c*' had grown about 8 cm. The three laterals were then drawn and are shown in Fig. 1.
The outlines of the stems were traced round and only the details were drawn freehand.

This last experiment added the further point that hetero-auxin paste applied to the
tip of a defoliated lateral prevented it from curving up and so in this respect replaced
the action of the young leaves, though it did not keep the lateral growing at the normal
rate, perhaps because it was not concentrated enough. But this effect of hetero-auxin
paste needs to be confirmed, since only the one lateral was tested with it, other tests
having been prevented by the failure of the plants of this species grown in pots.

It was next desirable to determine whether the defoliation of the plagiotropic laterals
checked their growth by making them susceptible to correlative inhibition. So in three
Impatiens plants (*a*) eleven laterals in all were deprived of their leaves, including those
only 1 or 2 mm. long, and the apical parts of the main shoots were left intact, while in
two other plants (*b*) eleven similar laterals were similarly defoliated but the apical parts
of the main shoots and all other laterals were cut off. Any more leaves which began to
develop later from the buds of the defoliated shoots were removed in turn.

After 14 days the mean growth of the 11 defoliated laterals was as follows: in (*a*)
1·55 cm. (extremes 3·1 and 0·9), in (*b*) 10·4 cm. (extremes 13·5 and 6·9).

In (*a*) the defoliated laterals had now nearly or quite stopped growing and were not
developing any more leaves, whereas in (*b*) they were still growing and developing leaves
rapidly.

So it was only when the main shoot was intact and growing that defoliation strongly
checked and finally arrested the laterals, and it therefore did so by making them susceptible

to correlative inhibition, just as did the defoliation of the orthotropic pea and bean shoots. The defoliated laterals again curved upwards very conspicuously in all the plants.

It is clear that the intact plagiotropic laterals in this species are not much inhibited by the main apex since they grow out strongly, but it was of interest to determine whether they are inhibited at all. So in each of two *Impatiens* plants (*a*) three laterals of one whorl were selected for observation and the apical parts of the main shoot were left intact, while in another similar plant (*b*) three similar laterals were selected, but the apical parts of the main shoot and all other laterals were cut off.
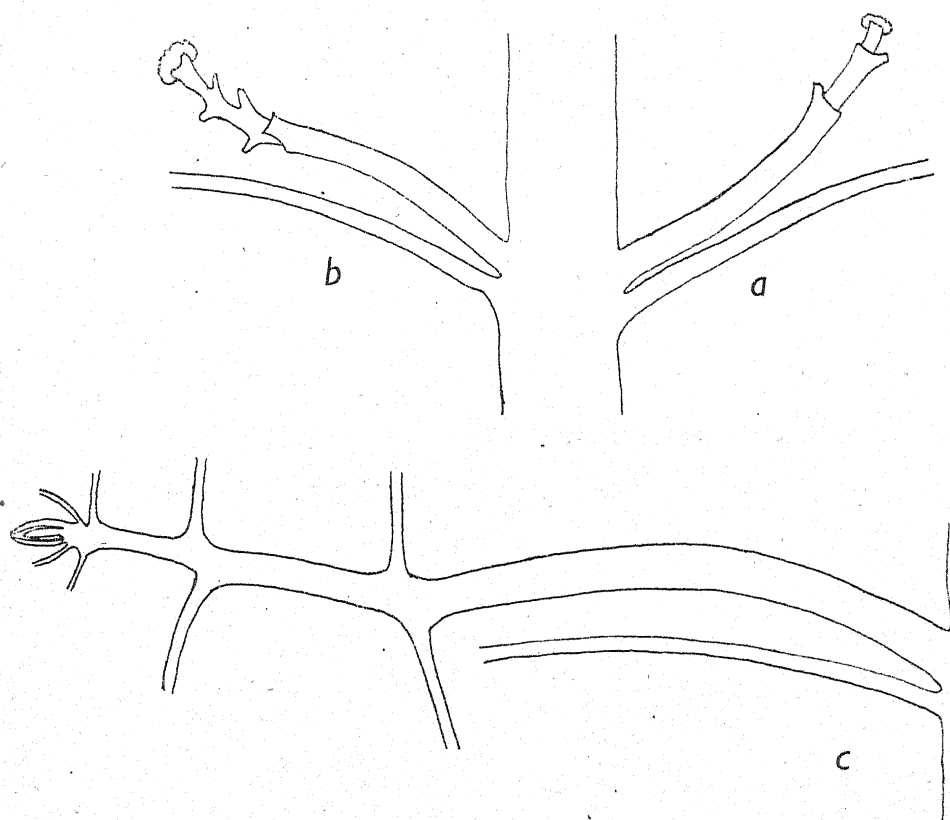
Fig. 1. *Impatiens Roylei*, three lateral shoots of one whorl. *a*, defoliated and capped with vaseline; *b*, defoliated and capped with hetero-auxin paste; *c*, intact. Only the petioles of the remaining leaves are shown.

In 10 days the laterals grew as follows:

In '*a*' (cm.): 10·3, 9·7, 9·7, 7·5, 6·5, 6·4 (mean 8·3).
In '*b*' (cm.): 9·8, 8·8, 8·4 (mean 9·0).

So the intact laterals are not appreciably inhibited by the main apex.

It is now time to review the results obtained with *Impatiens Roylei*. The epinastism of the intact laterals, which balanced against negative geotropism keeps them plagio-tropic, is induced by the main apex, and the first stage in the process of induction is the secretion of auxin by the main apex, as also it is known to be in correlative inhibition. For hetero-auxin paste applied in place of the main apex was found to induce epinastism

in laterals of *Impatiens*, as also it did in *Eupatorium cannabinum* (Münch, 1938). But intact *Impatiens* laterals are not inhibited by the main apex.

Defoliated laterals, on the other hand, are quickly inhibited by the main apex and finally arrested, but they are not made epinastic by it, or much less so, since they curve strongly upwards. So in both respects they react more like the orthotropic laterals of other species, such as pea and bean seedlings.

These results make it seem more probable that in shoots of this kind induced epinastism and correlative inhibition are alternative reactions to the same transmitted influence, in agreement with the conclusion of Münch that they are equivalent: for just when epinastism diminishes then inhibition develops, and this would be less likely to happen if they were reactions to two different influences transmitted simultaneously.

In some other species also it was found that plagiotropic laterals rose when defoliated or when darkened, or both. Thus in seedlings of *Salvia coccinea* grown in pots, in which the laterals grow out rather regularly at oblique upward angles and at the same time develop distinct epinastic curves, one lateral of each of nine pairs was deprived of its leaves, including those of small size, while the opposite lateral was left intact. Five of the nine defoliated laterals were also enclosed in black paper to diminish their production of auxin still more. After times of only from 4 to 7 days the defoliated laterals had all risen by diminishing their epinastic curves, the mean rise being 18° (extremes 32 and 10°), while of the intact laterals only one had risen, three were unchanged, and five had sunk, the mean change of angle being 6° down (extremes 25° down and 15° up). Also four laterals that were enclosed in dark paper without being defoliated all rose distinctly, the mean rise in 10 days being 16°.

In some young Douglas firs also four young lateral shoots were defoliated in May, when they had just emerged from the winter buds and were only 2 or 3 cm. long. These young shoots normally grow out fairly straight at angles of about 45° above the horizontal. After 17 days three of the defoliated shoots had curved upwards to the vertical and the fourth to an angle of 70° above the horizontal. Two rather longer shoots, about 6 cm. long, also curved up when defoliated, but more slowly.

In *Helianthus tuberosus* also defoliated laterals were found to rise slightly, but in *Fuchsia* and *Coleus* they did not change their angles. In *Salvia coccinea* and *Helianthus tuberosus* the intact laterals curve up when the main apex is removed, though only slowly in *Salvia*, but in *Fuchsia* and *Coleus* they do not.

It is well known that the plagiotropic lateral shoots of many species rise in the dark by negative geotropism, and references are given by Rawitscher (1932, pp. 94, 247, 249). The fact that in some species they rise when deprived of their developing leaves makes it probable that the cause is somehow the diminution of auxin, since both operations are known to diminish the formation of auxin greatly. This probability is increased by the experiment in which a defoliated *Impatiens* lateral was capped with hetero-auxin paste.

Some further experiments were made on lateral shoots of *Salvia coccinea* in order to determine how defoliation and darkening would modify their epinastism and negative geotropism if these were made to act separately. This was done by the well-known method of placing the plants, which were in pots, horizontal with the laterals that were to be observed on their sides, so that their epinastism now worked horizontally while their negative geotropism of course still worked vertically. One lateral of each pair was defoliated as before, and often it was also enclosed in dark paper, while the opposite

lateral was left intact; and the plant was then usually left for a few days before being placed horizontal, in order that most of the auxin remaining in the defoliated shoot might have time to move out of it. The geotropic curves were observed after times of less than one day, but it was made possible to observe the epinastic curves for one or more days by rotating the plants through 180° in the mornings and evenings so that the geotropic curves were continually reversed and did not become large enough to interfere.

Amongst fourteen pairs of laterals so treated it was found that the intact shoots all made strong epinastic and geotropic curvatures when placed on their sides, and the mean curvatures of the two kinds in the periods of observation happened to be equal, being both 53°. The defoliated laterals also made both epinastic and geotropic curves, but these, except in one shoot, were regularly less strong than were in the same periods those of the opposite intact laterals, though they were also considerable. The mean of the epinastic curvatures of the defoliated laterals was 29°, and of their geotropic curvatures 32°.

So the epinastic curvatures made by the laterals when placed on their sides were not significantly *more* diminished by defoliation than were the geotropic curvatures, though such a difference might have been expected from the rise of defoliated laterals in erect plants; for the small difference actually found in this sense is not significant. But the curvatures varied so greatly that there may be a genuine difference between the effects of defoliation on epinasty and geotropism, even if in this experiment it was too small to be detected; and moreover it is well known that for comparing the strength of two stimuli a comparison of the curvatures which they cause when acting separately is not a good method, since the curvatures may be limited by some other factor.

But in another respect these results are of interest. For Münch (1938, p. 668) has sought to draw the distinction that epinasty and inhibition of laterals are (directly or indirectly) provoked by ('erregt durch') the auxin of the main shoot, whereas their geotropic curvatures depend on ('beruhen auf') the auxin which they make themselves. But the present results indicate that the auxin which the laterals themselves make in their young leaves is needed about equally for their epinastic and geotropic curvatures. It is true that the first stage of the process by which the main shoot induces epinastism does not depend on the auxin made by the laterals, since the first stage is the secretion of auxin by the main apex. But then neither does the first stage of the geotropic process depend on the auxin made by the laterals, since that is the perception of the stimulus of gravity.

Whether or not correlative inhibition and the epinastism which leads to plagiotropism are alternative reactions to the same transmitted influence, it is certainly a rather general rule that, in buds and shoots inserted laterally on orthotropic main shoots, liability to correlative inhibition and plagiotropism, whether induced or permanent, are inversely correlated; and often they quite exclude each other, though some shoots, such as those of *Eupatorium cannabinum* on which Münch experimented, may be in an intermediate condition and liable to a little inhibition and a little induced epinastism also. This is especially clear in species with vegetative lateral buds of two kinds, those which are not inhibited by the main apex and grow out to form plagiotropic lateral shoots, and those which are inhibited and do not grow out unless the main apex is injured, but then form orthotropic shoots which replace it. Various such species, nearly all of them unfortunately tropical, have been investigated and described by Raciborski (1901), Massart (1924 *a*, *b*),

Sandt (1925) and Arndt (1929), of whom Massart has described the greatest number and has done so especially well and clearly. The rule that the orthotropic buds inserted on the main shoot are inhibited by the main apex, while the plagiotropic buds inserted on it are not inhibited, holds good even when both are formed in the same axils.

However, plagiotropic lateral buds may be inhibited when they are inserted on plagiotropic branches. This is clearly shown by the reactions of *Araucaria excelsa* which have been beautifully investigated by Massart (1924 *a*). For in that species not only does the main shoot form orthotropic replacement buds which are inhibited, and plagiotropic buds which grow out and form branches; but the branches behave in a corresponding manner, forming replacement buds which are inhibited by the apex of the branch and other buds which grow out and form branches of the second order, which are visibly different. The inhibited replacement buds formed by the branches are of course plagiotropic, and similar buds are formed by the branches of *Coffea arabica* and *Catha edulis* also (Sandt, 1925, p. 86). So the general rule seems to be not that plagiotropic buds are free from inhibition, but that those buds are free from inhibition which form shoots of a lower order than that of the shoot on which they are inserted.

This rule may even be extended tentatively to include lateral organs of two other kinds. For, in general, leaves and lateral flowers are either not liable to correlative inhibition or anyhow much less so than orthotropic vegetative buds of the same plants: and both leaves and lateral flowers are in general plagiotropic and may be considered as being of lower order than the stems bearing them.

The functional value of these arrangements is clear enough; for leaves, flowers, and those lateral shoots which are of lower order than the parent shoots perform their normal functions while the apex of the parent shoot is present and growing, whereas it would be disadvantageous if replacement buds were to grow out except when the apex of the parent shoot were injured. So it is very probable that these arrangements have been evolved by natural selection. But the physiology of the way in which the condition of being of lower order forms an alternative to inhibition or a protection against it certainly deserves to be further investigated. Extractions of auxin, such as Münch (1938, p. 669) proposed, are badly needed. It might also be considered whether his idea of the equivalence of induced epinastism and inhibition could be modified and extended so as to apply to laterals inserted on plagiotropic branches also.

SUMMARY

1. In decapitated seedlings of *Impatiens Roylei* a cap of hetero-auxin paste can replace the main shoot apex in making the lateral shoots epinastic, as Münch (1938) has found in *Eupatorium cannabinum*. Epinastism, as is well known, prevents lateral shoots from curving up by negative geotropism and so keeps them plagiotropic.

2. The plagiotropic laterals of *Impatiens Roylei* are not inhibited at all by the main shoot apex, but if they are deprived of developing leaves they become more nearly orthotropic and are then inhibited by the main apex like the normally orthotropic laterals of other species.

3. In various other species also the plagiotropic laterals rise when similarly defoliated or darkened or both.

4. In plagiotropic laterals of *Salvia coccinea* when the epinastism and negative

geotropism are acting in different planes, they are both diminished greatly by defoliation and darkening.

5. The results are discussed and it is considered that they make more probable the conclusion reached by Münch (1938) that induced epinastism and correlative inhibition are equivalent. It is further pointed out that in any case plagiotropism and liability to correlative inhibition exclude each other in the lateral buds of the orthotropic main shoots of a wide range of species, and also in lateral organs other than shoots. But some plagiotropic buds inserted on plagiotropic branches are inhibited, and a more general rule is proposed to cover these also.

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NUCLEAR PHASES AND ALTERNATION OF GENERATIONS IN *DRAPARNALDIOPSIS INDICA* BHARADWAJA

By RAMA NAGINA SINGH, M.Sc.

Department of Botany, Benares Hindu University

(With 49 figures in the text)

Since the investigation on the reproduction in *Draparnaldiopsis indica* Bharad. was completed (cf. Singh, 1942), a further study from a cytological standpoint has been in progress. A preliminary note (cf. Singh, 1943) was published in 1943, where it was stated that there are two kinds of plants, those producing gametes and others which form only asexual swarmers. These plants, although appearing identical outwardly, differ considerably in their cytological constitution. The gametophyte, possessing four chromosomes, represents the haploid phase, while the sporophyte with eight chromosomes is the diploid one. As mentioned in the note referred to above, the alga possesses an isomorphic alternation of generations. The present communication deals with the complete nuclear cycle involved in the life history of this plant.

MATERIAL AND METHODS

The material used in the present investigation was collected from shallow ponds near the villages of Pahari and Kadipur, about 4–6 miles from the Benares Hindu University grounds, during rainy seasons over a 3-year period. Plants were collected in the evening and brought to the laboratory. They were then fixed at half-hourly intervals during the following night after having been smeared with Belling's iron aceto-carmine (cf. La Cour, 1937). The chromosomes did not take the stain deeply, probably because of the abundant mucilage in which the filaments of the alga were embedded. Nuclear phases were found in great abundance in the material fixed between 10 p.m. and 2.30 a.m.

The fixatives employed were: (1) Navaschin's fluid, (2) a saturated solution of mercuric chloride in 70% alcohol (used hot), (3) alcohol-acetic acid, and (4) all the various modifications of Bouin's fluid (picro-formol mixtures). The best results were obtained with Navaschin's fluid and alcohol-acetic acid, the latter containing absolute alcohol and glacial acetic acid in equal proportions. For permanent aceto-carmine preparations, the latter fixative proved to be more satisfactory. The material was fixed in this mixture for about 24 hr., and when it was not to be used for staining immediately, it was stored in 70% alcohol. The following schedule, a modification of the one used for anthers, was employed for making permanent aceto-carmine smears: (1) a small amount of the material, either directly from the fixative or from that stored in 70% alcohol, was crushed in a drop of aceto-carmine on a clean slide with the help of an aluminium needle holder; (2) all debris was removed under the microscope before lowering the cover-slip; (3) the slide was heated gently over a spirit flame which dried the excess aceto-carmine, making a rim round the edge of the cover-slip, thereby facilitating its replacement afterwards in the original position; (4) the slide with the cover-glass directed downwards was then

placed in a ridged dish containing equal parts of glacial acetic acid and absolute alcohol. After 5–10 min. the cover-glass separated from the slide and sank to the bottom of the dish. After separation the slide and cover-glass remained in the mixture for an additional 5 min.; (5) the slide and cover-glass were next placed in two changes of absolute alcohol (5–10 min. in each), and then in the following grades of absolute alcohol and xylol, 5–10 min. in each: three parts of absolute alcohol and one part of xylol; equal volumes of alcohol and xylol; one part of alcohol and three parts of xylol; and finally in pure xylol; (6) the slide was next removed and a drop of canada balsam was placed on it. The cover-glass was also removed and was put back on the slide as far as possible in its original position, with the right side up. Care was taken to accelerate the process in order to avoid absorption of water by the medium and consequent clouding. In some cases when cloudiness appeared, it was removed by keeping the slide on a hot-plate for a short time.

Among the various stains used, Heidenhain's iron-alum haematoxylin proved to be the best. The material was either directly stained and mounted, or microtomed. In the former case, the method proposed by Carter (1926) for making preparations *in toto* was followed. The material fixed in acetic alcohol was usually left in the fluid from a few minutes to 24 hr. It was subsequently washed in several changes of 70% alcohol until all traces of acetic acid were removed. The material was next brought down gradually to water and washed in running water for 10 min. A small portion of this material was flooded in water on a slide smeared with a very thin layer of either Mayer's albumen fixative or Haupt's gelatin fixative (cf. Haupt, 1930). After draining off the surplus water, the slide was allowed to dry thoroughly and was subsequently treated exactly in the way in which we deal with paraffin sections. For microtoming, the fixed material, after having been washed in 70% alcohol, was gradually taken up through a series of alcohols and xylol, and then embedded in paraffin (m.p. 52–53° C.), and cut into sections 2–6μ thick. The following schedule for staining proved most satisfactory: (1) after bringing down the material to water, wash in running water for 10 min.; (2) mordant in 4% iron-alum (pure violet crystals being used, aqueous solution), 1 hr.; (3) wash in running water, 10 min.; (4) rinse in distilled water; (5) transfer to $\frac{1}{4}$% aqueous solution of Heidenhain's haematoxylin and stain for 12 hr. overnight; (6) wash in running water, 10 min.; (7) destain in a saturated aqueous solution of picric acid, until proper differentiation is secured; (8) wash in running water, 1 hr.; (9) dehydrate through a gradual series of alcohol grades, 5–100%, about 10–15 min. in each; (10) clear in clove oil and xylol; and (11) mount in neutral balsam.

CELL ORGANIZATION

Each cell contains a single nucleus and a single parietal and reticulate chloroplast with several pyrenoids (Fig. 11 *c*). In the main axis the nucleus usually lies close to the longitudinal cell wall in the peripheral protoplasm (Figs. 1–3), while in the laterals it is mostly present in the centre of the cell (Fig. 2 *a*).

The nuclei are generally 2–3μ in diameter, and in the cells of the ultimate laterals are not easily recognized. When occupying a central position they are suspended in the cell by strands of cytoplasm which stain rather deeply (Fig. 2 *a*). The nucleus, on account of a dark cytoplasmic girdle (Figs. 1–3) often found round it, is easily distinguished from a pyrenoid, but the nucleolus often stains in exactly the same way as the central body of the pyrenoid. In material fixed in the late afternoon (4.30–6 p.m.) many cases of division

were seen, but mitotic figures occur most abundantly in material fixed about 10.30 p.m. All the cells of a filament do not divide simultaneously. In a branch consisting of six cells, the lowest cell may contain a resting nucleus, the next above a dividing nucleus, and the four upper cells may show signs of recent division.

SOMATIC MITOSIS IN THE GAMETOPHYTE

The gametophytic plants, collected directly from nature, showed abundant nuclear division, both in the main axis and the laterals. In fixed and stained preparations, the swarmer-producing region appears much more deeply stained than the rest; this is evidently due to the denser protoplasmic content of the former, which is obvious even in unstained specimens.

Each resting cell of the gametophyte contains a single nucleus with a small nucleolus which stains deeply, while the reticulum is exceedingly delicate and difficult to distinguish (Figs. 1, 2). The cytoplasm is very conspicuous owing to the large number of vacuoles. The most characteristic feature of the resting cell is the constant presence, in close contact with the nucleus, of a darkly stained mass of dense cytoplasm, which is more or less definite in outline, although varying slightly in thickness and shape from cell to cell. Except in a few cases, it is polygonal. Such a cytoplasmic mass or girdle in close proximity to the nucleus has already been recorded by Carter (1926) in *Ulva lactuca*, by Ferguson (1932) in *Draparnaldia glomerata* and by Ramanathan (1939) in *Enteromorpha compressa*. These workers regard this mass merely as a localized accumulation of cytoplasm. With this interpretation the present author agrees, as it cannot be traced during the process of nuclear division.

As mitosis commences, the nucleus enlarges until it is nearly two or three times its original size; simultaneously there is a slight enlargement of the nucleolus, and a definite reticulum, bearing numerous chromatin granules at the angles of the network, appears (Figs. 2, 2 a.) No spireme was observed. The chromatin granules gradually become fewer but increase in size, owing to coalescence. Finally, four chromatin threads attached to the deeply stained nucleolus and extending up to the nuclear membrane are formed (Figs. 2, 2 a). These chromatin threads are the forerunners of the chromosome initials. It is by the condensation of these threads that the chromosomes are formed. The condensation process starts at the ends nearest to the nuclear membrane and proceeds gradually towards the nucleolus (Figs. 3, 3 a). Finally, when the condensation is complete, the condensed products become merged into the body of the nucleolus (Figs. 6, 6 a). The nucleolus fragments (cf. Westbrook, 1935) and possibly adds to the chromatin of the chromosomes, as the latter become organized exactly at the place where the nucleolus was located (Fig. 5). This hypothesis, although contrary to orthodox opinion, is further substantiated by the fact that the nucleolus loses its individuality and disappears completely after this stage of nuclear division. Whether the nucleolus adds to the chromatin of the chromosomes or not, the behaviour of the nucleolus here described, with the four chromosomes attached to it at the initial stage, does not appear to have so far been reported in algae and particularly not in Chlorophyceae. It may be that this behaviour of the nucleolus is a variant of that already described by Geitler (1930, 1934, 1935) and Suematsu (1936) in the genus *Spirogyra* and by Svedelius (1937) in the red alga, *Lomentaria rosea* (cf. also Gates, 1942). The four chromosomes ultimately formed are seen
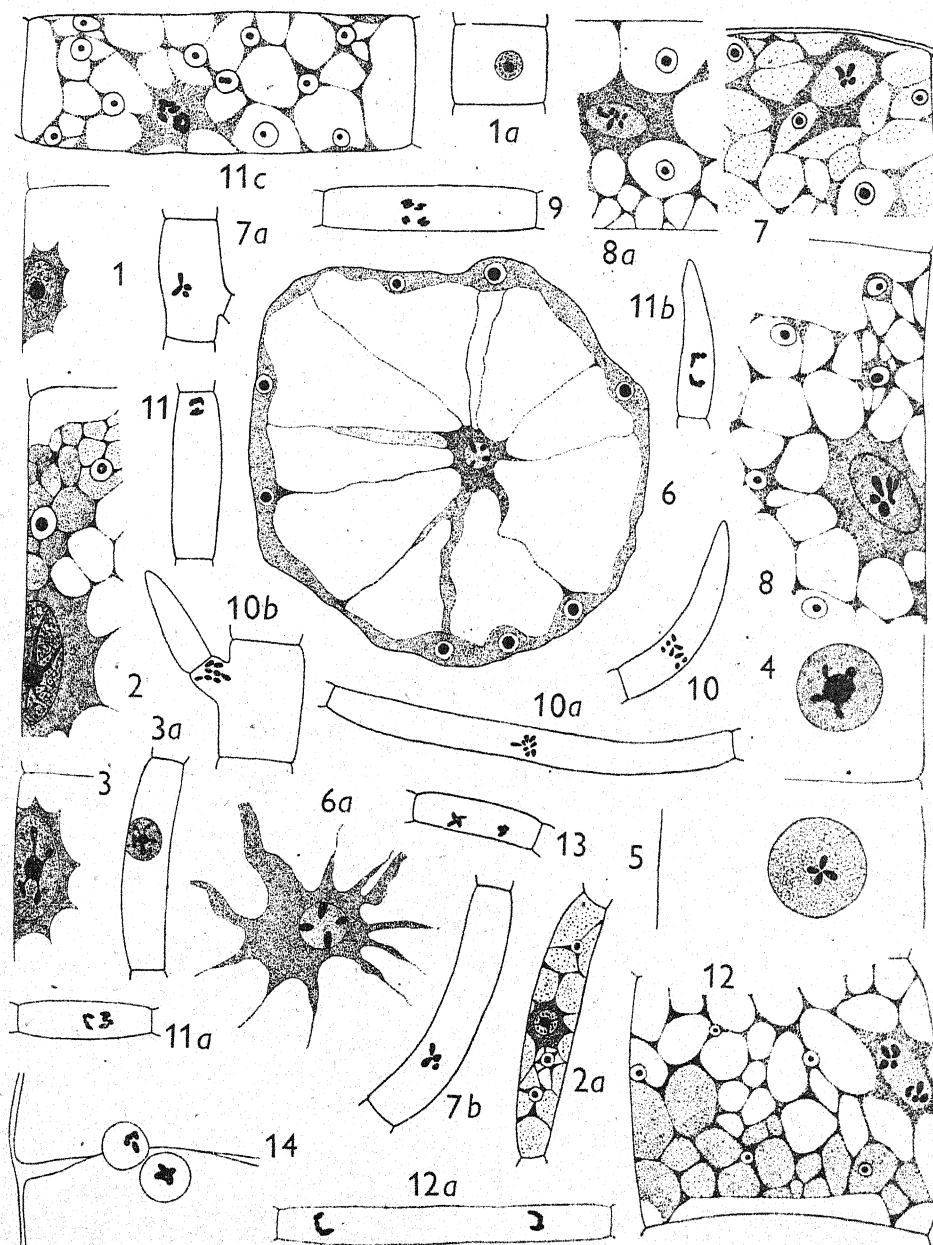
Figs. 1–14. Stages in somatic mitosis in the gametophyte. 1, 1 a, showing resting nucleus; 2, 2 a, early prophase, four distinct chromatin threads attached to the nucleolus; 3, 3 a, condensation of the chromatin threads; 4, a further stage of condensation; 5, formation of four chromosomes exactly at a place where the nucleolus was originally present; 6, 6 a, merging of condensed products into the body of the nucleolus; 7–7 b, late prophase showing four chromosomes and the complete disappearance of the nucleolus; 8, 8 a, splitting of chromosomes; 9, all chromosomes have split; 10–10 b, metaphase plates, polar view; 11–11 c, late anaphase; 12, 12 a, telophase; 13, late telophase; and 14, organization of daughter nuclei and formation of septum. All figures from whole mounts excepting 6 and 6 a, which are microtome sections. Fig. 6, × 1600; 6 a, × 3200; and the rest, × 1545.

clearly in the light unstained area in the cytoplasm originally occupied by the nucleolus (Figs. 5, 7 and 7 a). At the same time the nuclear membrane becomes very faint. The chromosomes are small almost rounded bodies or very short rods (Figs. 7, 8). They show signs of fission at an early stage (Figs. 8, 8 a). Fig. 8 shows a case in which one of the chromosomes has split across before metaphase.

At metaphase the chromosomes are arranged in one plane and are easily counted (Figs. 10–10 b). All the chromosomes have split, so that eight bodies lying in pairs can be seen in the clear unstained area (Fig. 9). There is no spindle formation, but the daughter chromosomes arrange themselves in the centre of the elliptical or circular unstained cytoplasmic area originally occupied by the nucleus and in such a manner as if they were arranged on the equatorial plate of a spindle (Figs. 10, 10 a). These chromosomes are of various shapes (Figs. 10–10 b), as is clearly seen in the axis cells where the nuclei are bigger and the chromosomes longer (Figs. 7, 8).

Before the separation of their halves, the chromosomes are oriented parallel to the longer axis of the cell. At an early stage of anaphase, the daughter chromosomes of a set show a tendency to coalesce and sometimes actually form a ring before moving apart from the other set (Figs. 11–11 c). In the axis cells, the movement of these coalesced masses, sometimes complete and sometimes incomplete, is restricted to a shorter distance (Figs. 11 c, 12), while in the cells of the laterals the rings of chromosomes move far apart, sometimes up to the opposite cross-walls limiting the cell (Fig. 12 a).

At telophase, the chromosomes generally clump together and gradually lose their identity. The nuclear membrane begins to reappear while the chromatin is still in irregular masses, and is fully formed when the nucleolus is reconstituted (Figs. 13, 14). A recently formed nucleus has a large nucleolus which takes an intense stain, but later the body of the nucleus becomes somewhat granular, the nucleolus losing its marked affinity for haematoxylin, when the resting condition is reached. The new wall is not laid down during nuclear division, but extends inwards as a collar from the original cell wall (Fig. 14). Ultimately it separates the newly organized daughter nuclei which at first lie close together in the middle of the cell in the main axis, but, as mentioned above, are far apart in the branch cells.

The pyrenoids vary in number, up to eight or more in the cells of the main axis, but two to five in those of the laterals (Figs. 2 a, 11 c). In stained material the pyrenoids differ considerably in appearance from time to time. Usually the effect produced is of a solid black mass surrounded by a white unstained sheath, the former representing the pyreno-crystal and the latter the starch sheath.

A correlation between the staining reactions of the pyrenoid and the condition of the nucleus has been noticed. When the nuclei are in the resting condition and barely take up haematoxylin, the pyrenoids are often deeply stained and are heterogeneous, with prominent unstained sheaths (Figs. 1, 1 a). When the nuclei are in active division, the pyrenoids are either small or very faintly stained (Fig. 11 c). During further stages they lose all their staining capacity and appear as pale bodies, only to be distinguished with difficulty. As the two daughter nuclei are organized, the pyrenoids gradually regain their staining capacity which is fully acquired when the two daughter cells are formed; the starch sheath also soon reappears (Fig. 41). This suggests that some stainable substance stored in the pyrenoids is used up during the formation of the chromosomes and is gradually restored to the former as nuclear division reaches completion. The pyrenoids

do not really disappear during division, but only lose a stainable substance, probably contained in an unstainable matrix, which is usually left behind.

This behaviour of the pyrenoids is similar to that recorded by Carter (1926) in *Mono-stroma* and *Ulva*, by Ferguson (1932) in *Draparnaldia glomerata*, and by Ramanathan (1939) in *Enteromorpha compressa*. Carter describes both a solution and a fragmentation of the pyrenoids with the dispersion of the fragments throughout the chloroplast, and suggests that both these processes may go on at the same time. Ferguson records only a fragmentation, Ramanathan only a solution process. The author's observations are in agreement with those of Ramanathan.
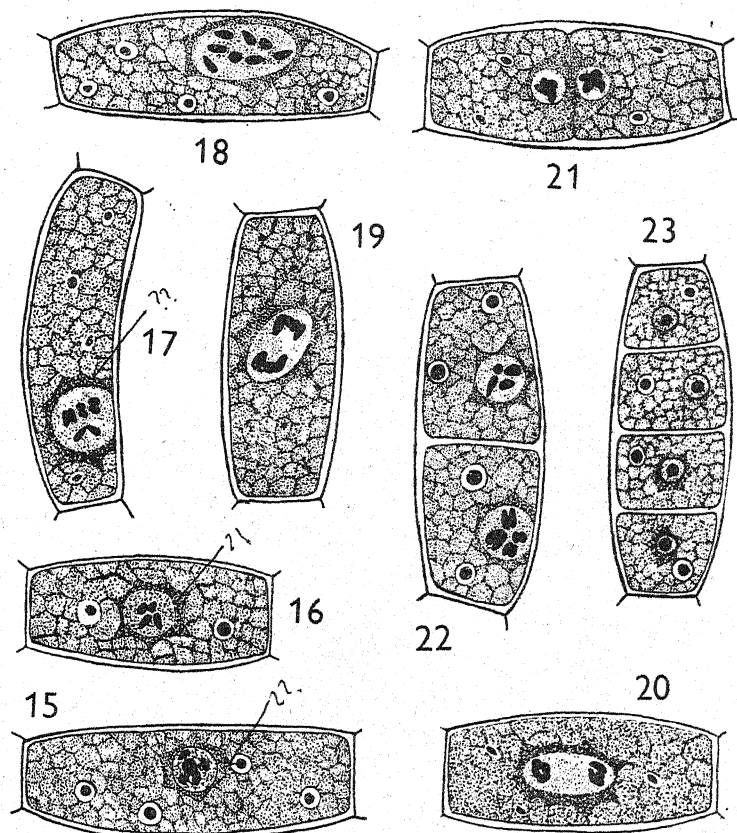
Figs. 15–23. Stages in nuclear division during gamete formation. 15, nucleus in prophase; 16, late prophase with four chromosomes; 17, metaphase; 18, anaphase, chromosomes beginning to orient; 19, late anaphase; 20, late telophase; 21, organization of daughter nuclei and formation of septum; 22, upper daughter cell in late prophase and lower one in metaphase; and 23, formation of gamete primordia. All × 2720.

GAMETOGENESIS

Any cell of the short laterals of the last two orders can give rise to gametes by division of its protoplast. Before the stage of actual gamete formation is reached, such cells show a greater accumulation of contents and become more deeply stained. The nucleus is small, measuring about 2μ in diameter and, like that of a vegetative cell, contains a deeply stained nucleolus and a very faint reticulum; there is also the same cytoplasmic mass associated with the nucleus (Fig. 15).

The nuclear divisions during gametogenesis resemble essentially those observed in vegetative mitosis, excepting that in some cases the products of division do not get separated by new transverse septa (Figs. 22, 23). On the other hand, after each nuclear division is completed, a cleavage of the protoplast takes place more or less simultaneously, so that at the end of each nuclear division uninucleate and somewhat angular primordia become constituted (Fig. 23). Only two such divisions (rarely more) have been observed in a cell (Fig. 23). When division is complete the primordia round off and assume the characteristic shape of the gametes (cf. Singh, 1942).
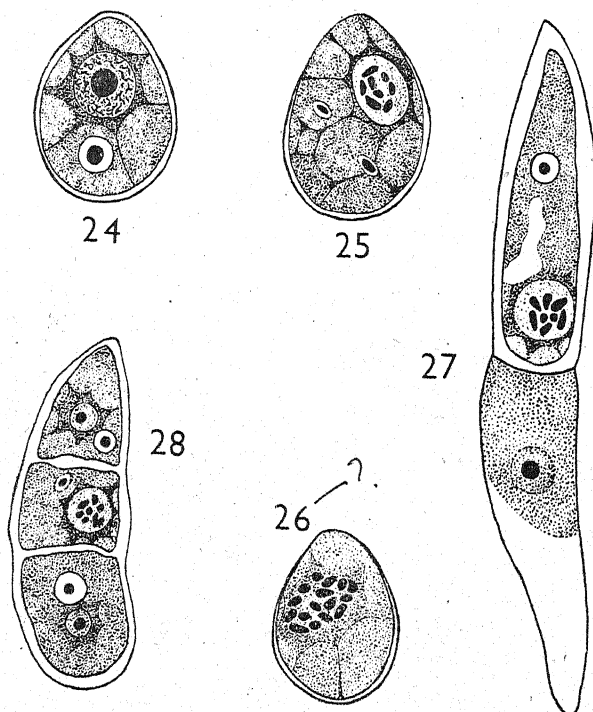
Figs. 24–28. Stages in nuclear division during the germination of zygotes. 24, early prophase; 25, late prophase; 26, metaphase, the chromosomes have already started to orient; 27, germling 3 days old with nucleus in the upper cell in prophase; and 28, a 4 days old germling with nucleus in the middle cell in prophase. All ×2720.

CYTOLOGY OF THE GERMLINGS FROM ZYGOTES

As the author stated in a previous communication (cf. Singh, 1942), the zygote germinates without undergoing any resting period. The young plants formed from the zygotes show abundant nuclear division, irrespective of the time of fixation, whether during the day or during the night. The nuclear divisions are quite similar to those found in adult plants collected from nature. Figs. 24–28 represent various stages of the vegetative mitosis in these germlings. The resting nucleus is like that of the somatic nucleus of the gamete-producing plant. At late prophase, one finds eight chromosomes, i.e. exactly double the number observed in the somatic nucleus of the gametophyte. The germlings of the zygotes are thus all diploid.

SOMATIC MITOSIS IN THE SPOROPHYTE

The cells are, in general, similar in asexual and sexual plants, although the resting nuclei as well as the dividing ones are often bigger in the asexual plants, being $3-4\mu$ in diameter as against $2-3\mu$ in the sexual ones. The vegetative mitosis in the sporophytic cells resembles in all respects that in the gametophyte. Eight chromosome units are organized in late prophase.
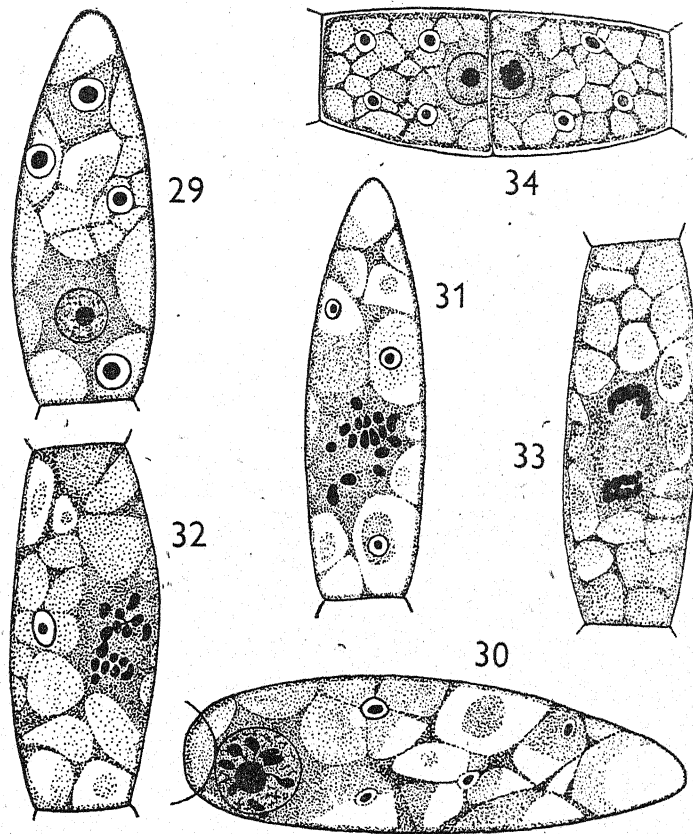
Figs. 29–34. Stages in somatic mitosis in the sporophyte. 29, early prophase; 30, prophase; 31, late metaphase; 32, anaphase; 33, telophase; and 34, organization of daughter nuclei. All × 2720.

ZOOSPOROGENESIS

The cells giving rise to zoospores differ only in their richer and denser contents. In early prophase the nucleus enlarges until it is three or four times the diameter of the resting nucleus (Figs. 35, 36). At the same time the reticulum becomes more prominent owing to the appearance of a number of darkly-stained chromatin granules at the junction of the fibrils (Fig. 36). The amount of chromatin increases gradually as some of the fibrils break apart and disappear, while others thicken and become more compact (Fig. 37). This thickening and condensation continues until eight chromosomes are formed. The chromosomes clump round the nucleolus and the latter then disappears. The chromosomes, though at first long and rod-shaped, gradually shorten and thicken, and then give
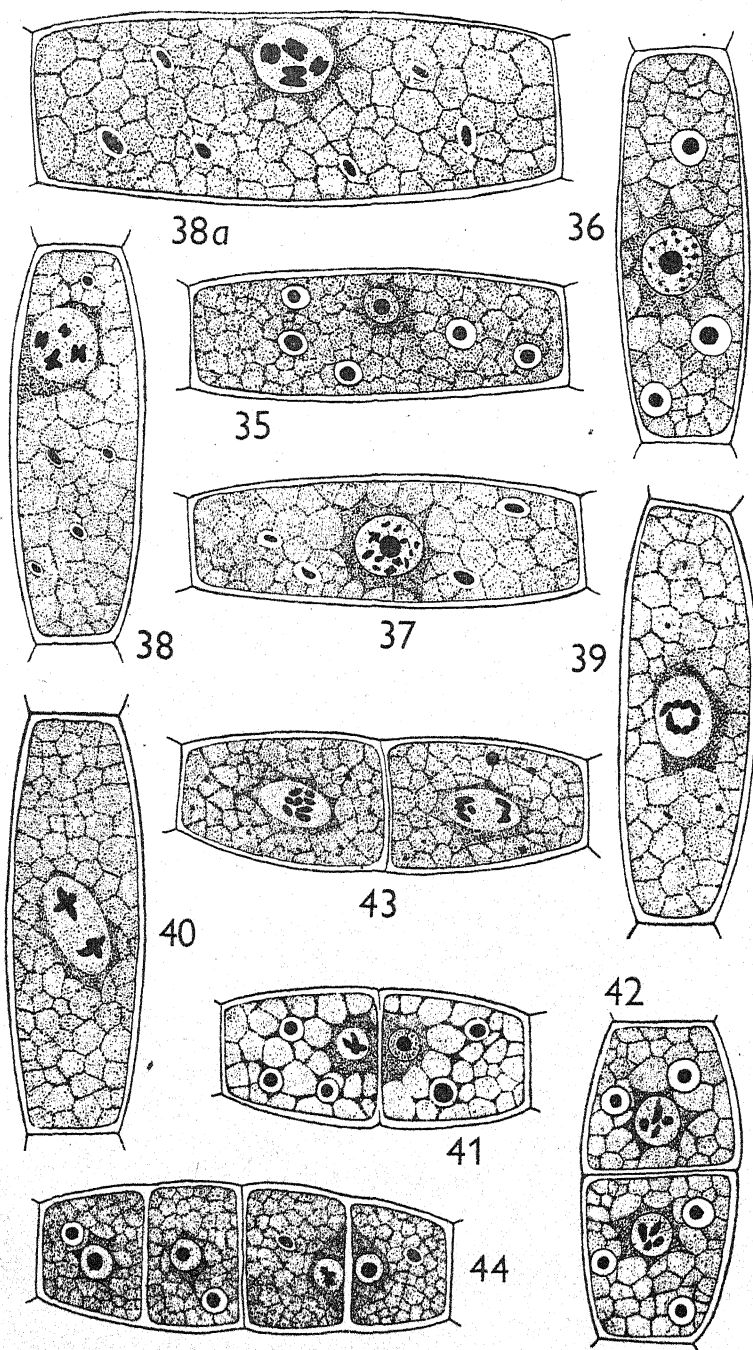
Figs. 35–44. Stages in the reduction divisions during zoosporogenesis. 35, resting nucleus; 36, early prophase; 37, late prophase; 38, 38 a, late diakinesis; 39, 40, early and late anaphase respectively; 41, telophase; 42, two daughter cells with nuclei in late prophase of the second division showing the four chromosomes; 43, one of the daughter cells in late metaphase and the other in late anaphase; and 44, formation of zoospore primordia. All ×2260.

rise to a distinct diakinesis phase which is, however, of very short duration (Figs. 38, 38 *a*). The number of bivalents is always four (Figs. 38, 38 *a*).

After the formation of bivalents, the nuclear membrane gradually disappears and the bivalents become arranged in the centre of the clear unstained cytoplasmic area, originally occupied by the nucleus (Figs. 38, 38 *a*). Anaphase and telophase follow rapidly one after the other, and the two daughter nuclei are soon organized (Figs. 39–41). Though the period of interkinesis is of very short duration, each nucleus organizes a nucleolus and a faint reticulum. A transverse septum is then formed before the second division commences (Fig. 41). The division of the two nuclei is in most cases simultaneous (Fig. 42), though occasionally successive. The homotype is similar to the ordinary somatic mitosis, except that four univalents (the reduced number) are recognized in the prophase (Fig. 42). Further divisions follow in quick succession, and usually occur simultaneously in all the nuclei. The cleavage of the protoplast again takes place, in the main, simultaneously with the nuclear divisions, and thin transverse septa are formed, so that the uninucleate zoospore-primordia appear either singly in each daughter cell or in twos (Fig. 44), fours or more. These primordia, at first angular, become rounded off and take on the characteristic shape of the zoospores (cf. Singh, 1942). The meiotic division is similar both in the region producing macrozoospores and the one producing microzoospores.

CYTOLOGICAL BEHAVIOUR OF THE ZOOSPORES DURING GERMINATION

The germination of the zoospores has already been described (cf. Singh, 1942). The abundant nuclear divisions shown by the germlings are quite similar in all respects to those observed in the adult gametophyte, there being four chromosomes (Figs. 45–49).
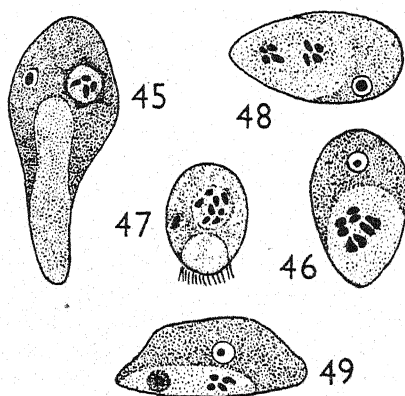
Figs. 45–49. Stages in nuclear division in the germination of zoospores. 45, late prophase; 46, early metaphase; 47, late metaphase; 48, late anaphase; and 49, telophase. All × 2720.

GENERAL DISCUSSION

The facts described in the foregoing pages show that there are two kinds of plants, the one producing gametes and the other zoospores. Although the two types of plants are exactly alike in outward appearance and are thus indistinguishable from each other, they can be differentiated by their chromosome number. The plants producing gametes, i.e. the gametophytes, possess four chromosomes and represent the haploid phase, while the sporophytes which form zoospores, contain eight chromosomes and represent the diploid generation. As shown in a previous communication (cf. Singh, 1942), the gametes, which contain four chromosomes, fuse only when they are from different plants. There is no morphological differentiation of the sexes. The zygotes germinate without undergoing any resting period and grow into plants, whose cells possess eight chromosomes. These plants produce only zoospores, preceded by a reduction division. The zoospores, after swimming for some time, settle down and grow into new plants, the cells of which possess four chromosomes and which, when fully grown, produce gametes.

There is thus a regular alternation of haploid (sexual) and diploid (asexual) generations
in the life cycle of *Draparnaldiopsis indica* Bharad. Since the two alternating phases
differ only in the number of chromosomes (2*n* and *n*) and in the type of reproduction
exhibited, the type of alternation of generations is isomorphic (cf. Fritsch, 1935, 1942).
The very close agreement between *Draparnaldiopsis indica* and *Ulothrix* (cf. Singh, 1942),
both in the methods of reproduction and in the simple filamentous structure of the
juvenile plants, with band-shaped chloroplasts in their cells, gives strong support to the
view put forward by Fritsch (1942) that the isomorphic phase alternation is derived from
the haploid type in one step, *Ulothrix* possessing a typical haploid life cycle.

While studying the mitotic divisions in *Draparnaldia glomerata*, Ferguson invariably
observed eight chromosomes in the cells. It was not possible for her to decide whether
this chromosome number represented the haploid or diploid condition. Although she
observed the liberation of countless spores, no cell produced much more than one spore
nor were any cases of fusion observed. She found variation in the sizes of the spores,
but this was explained as due to differences in the sizes of the parent cells, since the
smaller spores did not fuse and so did not behave as gametes like the microzoospores
described by Klebs. She adds: 'this absence of fusion between spores, a process very
frequently described, is somewhat puzzling. It may be that for certain conditions of
habitat or nutrition a purely asexual habit has become established, and that neither fusion
nor reduction takes place. Such a cycle might arise in either phase, and until nuclei
giving some other number of chromosomes are found, no further conclusion can be
reached.' In the light of the present investigations (cf. also Singh, 1942) it appears
probable that the life cycle of *Draparnaldia glomerata* involves the same nuclear phases
as those observed in *Draparnaldiopsis indica*. Ferguson perhaps examined only diploid
plants having eight chromosomes and because of this could not observe any fusion between
the spores, although she found differences in their size. The smaller zoospores were most
probably of the nature of the microzoospores of *Draparnaldiopsis indica* and therefore
asexual in behaviour. In view of the observations made by Ferguson (1932) on *Drapar-
naldia glomerata* and those of the author on *Draparnaldiopsis indica*, the statement of
Pascher (1904) (cf. also Fritsch, 1935) that 'the sexual role fulfilled in *Ulothrix* by the
biflagellate swarmer has been taken over in *Stigeoclonium* and *Draparnaldia* by the
quadriflagellate microzoospore', requires revision.

An interesting point in the cytology of *Draparnaldiopsis indica* is the behaviour of the
nucleolus, which becomes brightly stained and very conspicuous. With the commence-
ment of mitotic division, the nucleolus increases in size and four or eight (as the case
may be) chromatin threads get attached to it during early prophase. Finally, these
chromatin threads become condensed and the products get merged into the body of the
nucleolus. The nucleolus fragments and possibly adds to the chromatin of the chromo-
somes. The former then disappears and is indistinguishable during subsequent stages.
The chromosomes are formed exactly at the place originally occupied by the nucleolus.
A definite spindle is absent, as also stated by Ferguson (1932) in *Draparnaldia glomerata*.
Movement of the chromosomes takes place in the clear region in the middle of the cell,
and this agrees with the account of T' Serclaes (1922) for *Cladophora glomerata* and that
of Higgins (1930, 1931) for *Cladophora flavescens*. Carter (1926) found only a few doubtful
spindles in her investigation of the Ulvaceae, while Ramanathan (1939) found them quite
commonly in *Enteromorpha compressa*. In many respects (e.g. formation of chromosomes

without any spireme stage, the shape of the chromosomes, and the absence of a spindle) von Neuenstein's (1914) account of mitosis in *Microspora amoena* and Ferguson's (1932) account of *Draparnaldia glomerata* agree with that of *Draparnaldiopsis indica*.

The meiotic division in *Draparnaldiopsis indica* is in agreement with the one described by Svedelius (1937) in *Lomentaria clavellosa*. There is a typical and distinct diakinesis stage with four bivalents, thus indicating that a true reduction division has taken place.

SUMMARY AND CONCLUSION

An account is given of the nuclear phases and alternation of generations in *Draparnaldiopsis indica* Bharadwaja. A cytological study of the alga collected from nature shows that the sexual plants have four and the asexual ones eight chromosomes.

The germlings produced from the germination of the zygotes are diploid with eight chromosomes. The mature plants derived from zygotes produce only asexual swarmers. Reduction in the number of chromosomes takes place during the formation of zoospores. A typical diakinesis stage forms the conspicuous feature of this division. Four bivalents were observed in the first division and four univalents in the subsequent ones.

The zoospores develop immediately into haploid germlings with four chromosomes. The resulting plants produce only gametes.

There is thus a regular alternation between a haploid gametophyte and a diploid sporophyte, the two generations being externally exactly alike. *Draparnaldiopsis indica* Bharadwaja therefore shows an isomorphic alternation of phases.

In conclusion, I have much pleasure in expressing my great indebtedness to Prof. Y. Bharadwaja for his kind guidance and criticism throughout the course of this investigation.

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THE STRUCTURE AND REPRODUCTION OF THE VIRGIN FOREST OF THE NORTH TEMPERATE ZONE

By E. W. JONES

Imperial Forestry Institute, Oxford

(With 5 figures in the text)

Though the northern temperate and arctic forest regions are reasonably well known floristically, our knowledge of the more fundamental aspects of the ecology of their primeval forests is almost as scanty as that relating to tropical forests. In this paper an attempt will be made to review some features of the structure and reproduction of the north temperate virgin forests, and to consider their bearing on ecological theory. We shall also include some reference to arctic forests. The subject is a difficult one to approach, partly on account of the scarcity of intensive work in examples of virgin forest, and partly on account of the inherent nature of the subject; there is unlikely to be one rigidly definable and constant structure or method of reproduction, even within a single kind of forest, so that we can only hope to ascertain the prevailing characteristics.

THE CONCEPT OF VIRGIN FOREST

There has been some difference of opinion as to the limits of the term 'virgin forest' (Urwald). Some say that human interference should be altogether absent—a difficult condition to fulfil in countries which have been inhabited by man for many thousands of years. Others say that so long as there has not been deliberate modification of the forest by planned silviculture or systematic working it must be accepted as virgin; to use Schenck's vivid language primitive man 'ist genau so sehr zum Urwald gehörig, wie Hirsch und Elch und Caribou, und Urwaldbaume' (just as much part of the virgin forest as the stag and elk and caribou, and the trees of the virgin forest) (Schenck, 1924). Indeed, American writers (who often use the term 'old-growth forests') often include forests which have been cut over. Such forests may merely have had scattered stems of a single valuable species removed (e.g. *Pinus strobus* in the Lake States of U.S.A.) and be little affected otherwise; the condition before logging can sometimes be reconstructed from the distribution and size of stumps (e.g. Graham, 1941 *a*). Baseler (1932) and Zednik (1938–9) make 'Urwald' practically synonymous with climax forest—surely quite an unjustifiable limitation.

THE FIELD OF STUDY

The temperate forests have been so devastated and changed by man that the material left for study is very scanty. In central and western Europe even the original distribution of species such as *Pinus sylvestris* L. (Scots pine), *Quercus robus* L. (oak) and *Castanea sativa* Mill. (chestnut) has become a matter of uncertainty, and only one or two small fragments of untouched, or nearly untouched, forest remain. The most famous of these are the Bialowies forest in Poland, preserved as a hunting forest of the Russian Czars, and the Kubany Wald at Schattawa in the Bohemian forest, set aside by its owner,

Prince Schwarzenberg, in 1858 as a 'nature reserve'. I do not know of any intensive work in either, though general accounts exist (see Baseler (1932) for references), and it has been stated that both are far from being in a primitive condition on account of the abnormally high stocking with game. Much forest within the remoter mountain districts of France, Switzerland and the central European countries has only been brought under management during the past century or century and a quarter, and the early foresters must have been very familiar with nearly untouched forest; one or two descriptions have come down to us from this period (Seidel, 1848; von Berg, 1861; Wessely, 1853, etc.). Monasteries, in particular, maintained great massifs of uninhabited forest on their domains. Documentary evidence, such as that collected by K. Meyer (1941), emphasizes the fact that even in these, grazing and charcoal burning have been prevalent for many centuries, and that there have been great changes in the proportions of species during historical times. He tells of a seventh-century bishop of Lausanne who, when rebuilding a church in that city, had, even in that richly wooded district, to go 30 miles north into the centre of the Jura massif to get building timber—the presumption is that all the nearer woods were coppice.

In the Carpathians, the Balkans and Asia Minor, at higher levels, there are still stretches of unworked forest, and it is to these that most recent European students of virgin forest have gone. Sample plots have been measured and charted in detail by Markgraf (Markgraf & Dengler, 1931) in the Balkans, and by Mauve (1931) in the Carpathians. Mauve's work, which is some of the most important in this field, will be referred to more fully later. Cermak (1910) and Fröhlich (1930) both give some quantitative information on the Balkan forests, but their enumerations are much less detailed than those of Markgraf or Mauve. Baseler (1932) studied in Anatolia; his paper includes a very useful bibliography and historical résumé of earlier work on the temperate virgin forest which is particularly useful with respect to European work. Zednik also worked in Anatolia (1938–9), but his paper is of little importance; it contains very few original observations, and reproduces Baseler's bibliography with only one or two additions relating to Turkish forests. Müller (1929) also worked in Asia Minor, but practically all the examples he selected for study were relatively young stands in areas where there had been much human interference; his book contains few quantitative or detailed observations to demonstrate the elaborate schemes of species-succession which he postulates. His work has been severely criticized, e.g. by Hesmer (1930), and gives the impression of being uncritical.

In eastern and central North America the magnificent virgin forest has already been destroyed so completely that there are only tiny and often partly altered fragments left. There are rather larger areas in the west. American work on the problems under review has, however, been very scanty, and mostly comes from the eastern states. Cooper's work on the Lake Superior forests (1913), though some of the earliest, is still some of the most detailed quantitative work which has come from that country. Much of the later work has been published only in a very abbreviated condition.

There are presumably considerable areas of virgin forest in eastern Asia, and some of these have been studied by members of the Forestry Department of the University of Vladivostock. The only account of this apparently very extensive and important work which I have been able to consult is the account given by Iwaschkewitsch to the Congress of Forest Experiment Stations (1929a), and this, though very valuable, gives details of

only a small part of the work. Much of the arctic forest of Siberia and North America also remains untouched. This too has been little studied, but it is so much simpler that the broad facts of its regeneration and structure seem fairly clear.

SIZES AND AGES ATTAINED

Before examining the structure, some of the salient facts concerning the sizes and ages of trees, and the volume of timber present, will be summarized. Very commonly the age attained by the dominants seems to be about 300 years. This is about the usual maximum age for beech in the Carpathians (Mauve, 1931); *Abies alba* Mill. in Europe, and *Pinus koraiensis* in eastern Asia (Iwaschkewitsch) attain about 350 years. The dominants of the American forest reach a similar age—e.g. Nichols (1913) records the maximum age of *Tsuga canadensis* Carr. at Colebrook, Connecticut, as 350 years, and the average age at maturity as 275 years. Nevertheless, in both Europe and America ages up to 500 years appear to be not infrequent, but longer-lived species are exceptional. In the northern coniferous forest the dominants in general seem to be shorter-lived (Nichols, 1935), though pine (*Pinus sylvestris*) over 400 years old is recorded from Arctic Finland by Lakari (1915), and ages of over 200 are general. In the Isle Royale forest of Lake Superior, *Abies balsamea* Mill. reaches a maximum age of 120; Cooper (1913) regards this as the climax dominant, though it seems to be exceptionally short-lived for this. Graham (1941 a) rejects it as a possible climax dominant in the region a little farther south for this reason, although, with the much longer-lived *Picea glauca* Voss., it appears to be one of the dominants in the northern coniferous forest of eastern Canada.

Throughout Europe and much of North America the height attained under good conditions by the dominant species is very commonly about 100 ft. (30 m.), rising up to 150 ft. (46 m.) under exceptionally favourable conditions. Auten (1941) gives 97 ft. as the mean and 113 ft. as the maximum dominant height* in twenty-two virgin stands in Ohio, Indiana and Illinois. Beech and oak attain about this height in Europe; individual trees amongst the exceptionally fine oak of Bellême and Réno Valdieu in Normandy reach 40 m. There is often a species present which is capable of growing some 30–40 ft. taller than the majority of the species—such are *Pinus strobus* L. in eastern U.S.A., often attaining 140 ft., and *Abies alba* in Europe.

A very common maximum diameter for the dominants growing in closed stands is 40 in. (100 cm.), though again for certain species records of considerably larger diameters are not infrequent—e.g. *Pinus strobus* to 49 in. (125 cm.) (Lutz, Hough, Auten *et al.*), *Quercus sessiliflora* Salisb. to 150 cm. at Bellême. In the Northern Coniferous Forest sizes are much smaller. In northern Finland pine and spruce of 20 m. are very tall, while 14–18 m. is the usual height range at maturity. 49 cm. diameter at breast height is exceptional, while 25–40 cm. is usual (Aaltonen, 1919). These figures are probably typical of the Canadian Arctic also; diameters of 20 cm. are exceptional for *Abies balsamea* (Cooper).

The Pacific coastal forests of North America are unique in the northern temperate regions in having species such as *Thuja plicata* D. Don, *Pseudotsuga taxifolia* Britt., and the *Sequoias*, which attain far greater sizes and ages than those recorded above.

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* Mean height of dominant trees—using dominant in the forester's sense for the tallest height-class of trees.

It is difficult to give useful figures for the numbers of stems, since the diameter limits used in enumerations vary so greatly; volume figures are more useful. There can, however, be a great range in volume of timber, particularly for stands of even-aged character, and volumes for small areas are apt to be misleading since there are not infrequently small groups of trees of great size and age. In La Glacière, a fragment of a few hectares of unworked *Abies alba* forest in the Forêt de la Joux near Champagnole in the French Jura, the trees of the dominant stand are all over 200 years old, and the average volume per hectare is 584 cu.m., but over small areas it rises to 900 cu.m. Mauve found volumes (on 0·25 ha. plots) of up to 1154 cu.m./ha. in the Carpathians, and Fröhlich found up to 606 cu.m./ha. in the Balkans. Volumes usually seem to be lower than this however; Auten gives the average volume for his twenty-two American stands as 20,800 board ft./acre—this probably is about 2770 cu.ft./acre, or 193 cu.m./ha., the exact volume depending on the sizes of timber present. For comparison with these figures, about 350–400 cu.m./ha. may be taken as a figure often accepted by Continental foresters as satisfactory for managed selection forest where all ages of tree are present, though in actual practice volumes are often about 500 cu.m.

TYPES OF STRUCTURE

The structure and reproduction of the forest are intimately related; the method of reproduction largely determines the structure, and can to some extent be deduced from it. There are many conceivable types of structure, and it would clearly be a mistake to expect natural forest to conform too closely to any one pattern; indeed, it might even be so variable as to show no prevailing pattern. Some of the possible structures which might be expected will first be listed:

(a) Even-aged, single-storied, with a uniform closed canopy.

(b) Two or several age classes present, with few or no trees of the intervening ages. The age classes might be segregated (i) in separate stories, or (ii) in groups.

(c) All ages of stem present, intimately intermingled, with irregular, open canopy.

(d) All ages of stem present, but forming a mosaic of even-aged groups.

(e) All ages of stem present, but with regular uniform canopy and storied structure.

This list is not exhaustive, and intermediate conditions might of course exist, as, for example, an even-aged component of a stand mixed with an all-aged component. The first type of stand (a) has long been familiar, since this was the first kind of forest to be created by the early foresters, and was regarded by them as the ideal at which to aim. The crowns of the trees are all more or less on the same level, and although the range of height and crown length is rather greater with tolerant ('shade-bearing') species such as *Fagus* or *Abies* than with intolerant species ('light-demanding') such as *Larix* or *Betula*, there is no stratification of the crowns. (There may, of course, be an understorey of shrubby species of another life form.) The frequency-distribution curve of diameters of living stems is of the binomial type, and is usually skew (see Fig. 1). The canopy is regular, continuous and close. Crops which are even-aged or nearly so are often spoken of as being of 'uniform' character.

Type (c) is also well known to foresters as the form of managed 'selection forest' ('Plenterwald', 'Blenderwald', 'Forêt jardinée') in which all ages of tree are present everywhere and felling is confined to isolated scattered stems. In the ideal form at which

the forester aims a regular canopy scarcely exists; tree crowns overlap and intermingle at all heights. In profile the canopy is highly irregular, the peaks being formed by the oldest and largest trees standing up amongst their younger neighbours. The stem diameter distribution is of the falling logarithmic type. This form of forest has had a steadily increasing vogue during the past 60 or 80 years, but the believers in 'uniform system' and 'selection system' tend to be ranged in opposing camps and to hold exceedingly strong views on the subject. Most of the European foresters who have written on virgin forests have been interested in their bearing on silviculture, and in particular on this
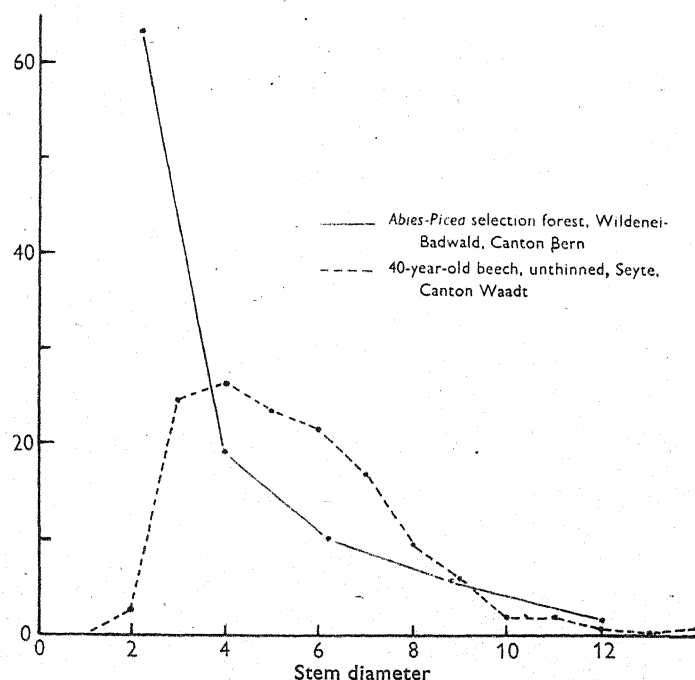
Fig. 1. Stem-diameter frequencies in managed selection forest (all ages of tree present) and in even-aged forest. The number of stems in each diameter class has been given as a percentage of the total number of stems enumerated, while the abscissa scale has been adjusted so that the diameter range occupies about the same length in each case. In the selection forest stems over 7 cm. diameter were enumerated, the total number above this diameter being 798 per ha. The maximum diameter was 72 cm., and the figures on the abscissa scale are one-fifth of the diameter in centimetres. In the even-aged beech there were 7740 stems per ha., and the enumeration was complete. The maximum diameter was 14 cm. and the figures on the abscissa give the diameter in centimetres. Figures from Flury (1929) and (1903) respectively.

dispute; hence their writings are not always quite free from bias. To the ecologist interest centres more upon problems of succession and the climax condition which will be more fully discussed in the final section of this paper.

　　Even-aged stands are apparently common in virgin forest, and are usually regarded as originating after fire. The closely allied form of stand in which there are a limited number of distinct age classes also appears to be frequent. In the arctic forest one of these two types of structure is the rule; Lakari (1915) gives many examples from old unmanaged forest in Finland, and Tkatschenko describes them from Russia (1929). Maissurow (1941) says that half the virgin stands of Wisconsin are even-aged, and Schenck (1924) emphasizes their wide distribution in North America. Many reports of even-aged stands

are doubtless based on appearance only, or at most on stem-diameter frequencies, which, as will be seen later, can be misleading. It is, moreover, usually impossible to determine the age of an old tree accurately within 15 or 20 years, especially when it has endured in youth all the hardships and misfortunes of a natural environment. Thus it is difficult to say exactly how even-aged these stands are. Lakari lists several Finnish stands where 88% or more of the trees are in the 157-year age class (i.e. from 153 to 162 years old), the remainder often being a hundred years or so older; indeed, in one stand 97% were in a single age class. His figures suggest, however, that stands with not more than 50–70% in one age class are far commoner; in such cases either the bulk of the stems fall into two or three consecutive age classes (i.e. there is an age range of perhaps 30 years) or else the stand is of the distinct age-class type (type (b), p. 133). Fires were mainly responsible for the age classes, though scarcity of seed years also contributed; thus in one case the fire (dated from scars on a few very old trees which had survived it) was 253 years ago, but the age of the pine crop arising after it was only 213–222 years. Cermak (1910) gives an example of *Fagus-Abies* forest in Bosnia in which 74% of the stems were from 161 to 190 years old, with a maximum frequency of 32% in the 171–180-year class; his figures are, however, based on only 30–50 age determinations on the larger stems.

Even-aged components of otherwise uneven-aged crops also seem to be common. Frequently these take the form of an over-storey of widely spaced individuals of great size standing in an uneven-aged matrix of other smaller species. This was the condition in which *Pinus strobus* very often occurred scattered amongst *Fagus*, *Acer* and *Tsuga* spp. in eastern U.S.A. (Hough, 1932; Lutz, 1930; Graham, 1941a; *et al.*). Farther west *Pinus monticola* Lamb. played a similar role (Schenck, 1924; Huberman, 1935, *et al.*). The forest of *P. koraiensis* from Manchuria (Iwaschkewitsch) presents in some respects an analogous case, though the pines were here sufficiently abundant to be dominant. Their age range was 170–250 years, but most were over 200 years old; they stood amongst younger and more tolerant species. One of Mauve's plots in the Carpathians (plot C) seems to show a more or less even-aged overstorey of *Picea* standing amongst younger *Abies alba*. This state of affairs strongly suggests that succession is still in progress, especially since the even-aged species is always relatively intolerant and not re-generating.

The even-aged group structure (types (b) (ii) and (d), p. 133), such as would be produced if the mass seeding-up of gaps made by wind- or snow-break were the usual method of regeneration, has not often been recorded. It is probably commoner than the available data suggest, however, since unless sufficiently obvious superficially it would easily pass unnoticed. Mere enumerations or age counts without some sort of charting would not reveal it. Cooper found the *Abies balsamea* forest of Isle Royale in Lake Superior was of this type, and Meyer & Saldana's transect diagrams (1937) of forests in the Mexican mountains (mixed *Abies religiosa* Lindl., *Pinus* spp. and *Quercus* spp.) appear to represent it. Probably group structure could be found developed to some extent, at least locally, in most forests. Rubner (1934), Fröhlich (1930) and Markgraf & Dengler (1931) all stress the abundance of small groups of regeneration filling gaps left by the collapse of one or several old trees in the *Fagus-Abies* forest of the Balkans, and yet so far as can be judged from their accounts, the forest as a whole does not show an even-aged group structure. This may partly be because the groups are mostly too small—Markgraf says they varied from about 100 sq.m. to a quarter of a hectare in area and about 50 m. apart—

and partly because they arise sufficiently rarely for the differences in size between the members of the older groups, which must form the bulk of the stand, not to be apparent. Iwaschkewitsch says that in the Usuri area in Manchuria which he studied, only one small patch of about three-quarters of a hectare could be found which showed the even-aged group structure.

All-aged forest with irregular canopy answering to the forester's picture of 'selection forest' (type (c), p. 133) appears to be rare. In the Carpathians, Mauve found it very locally in pure *Picea abies* forest on sandstone boulder-strewn slopes with shallow soils. Cermak (1910) also reports this structure in *Pinus leucodermis* Antoine forest on very steep rocky slopes in the Balkans. Hofmann (1913) describes it as of very local occurrence in Japan. It appears to develop only where irregularity of site or violence of climate impose irregularity of structure on the forest.

A far commoner form of uneven-aged forest has a regular continuous canopy and has very much the appearance of an even-aged high forest. It is perhaps too much to say that all ages are present, but although old stems predominate, the dominant stand includes a wide range of ages. In an example of a Bosnian beech forest given by Cermak the age range was 200 years, though nearly 70 % of the stems were between the limits of 170 and 200 years; the youngest stems were 90–100 years old. Regeneration in such forests often appears to be absent, and there is a striking deficiency of the smaller stems, giving a diameter distribution which may approach that of an even-aged stand. This, however, does not necessarily mean that the forest is not reproducing itself and maintaining its present structure; the condition doubtless arises through the relatively small fraction of the life spent in growing from ground-level into the canopy when a gap is formed. Where the average length of life is 300 years only two or three gaps per hectare, each containing one or two young stems, would be sufficient to perpetuate the forest.

All-aged forest can apparently show every degree of transition between the uniform-canopied 'even-aged aspect' forest just described to that in which there is a continuous canopy but a definite storied structure, the lower stories being often, but by no means always, formed by younger age classes. From this again there is every transition to the rarer irregular-canopied type of structure. Perhaps the 'even-aged aspect' forest is some-times a stage in the development of the storied type of forest; some of the statements of Mauve and Markgraf suggest this possibility, but without more work it would be impos-sible to decide the point. For the tolerant species which form the climax forest of Europe the storied structure or one of the intermediate conditions between this and the 'even-aged aspect' condition seems to have been usual. Wessely's early descriptions of the Austrian forest (1853) suggest one of these forms, and Markgraf's and Mauve's sample plots in *Fagus-Abies* forest show it in the Balkans and the Carpathians. It is also apparently by far the commonest form in North America (Schenck, 1924; Nichols, 1913; Lutz, 1930), in Japan (Hofmann, 1913) and Manchuria (Iwaschkewitsch, 1929a).

The frequency of even-aged components in forests of mixed ages has already been noted, and just as there are transitions in structure, so there is every transition between the true all-aged condition and the condition with distinct and sharply defined age classes. Indeed, some degree of differentiation of distinct age classes seems to be the rule. Even-aged components are by no means confined to the upper storey. Sometimes the various age classes are associated with different species.

Mauve (1931) and Iwaschkewitsch (1929a) have made by far the most detailed studies

extant of this kind of forest, and their work, which is important enough to merit fuller description, will serve to illustrate some of the above points.

Mauve worked in the forest near Majdan in Poland, on the northern slopes of the Forest Carpathians. Seven sample plots in various kinds of forest were charted in great detail, heights, diameters and ages of all trees being recorded in several of them. The most widespread and 'central' type of forest was of mixed *Fagus sylvatica* L., *Abies alba* Miller and *Picea abies* Karst., and as the height-class figures show, was distinctly two-storied (cf. plot A, Fig. 2), even though all ages up to 300 years were present. The stem diameter
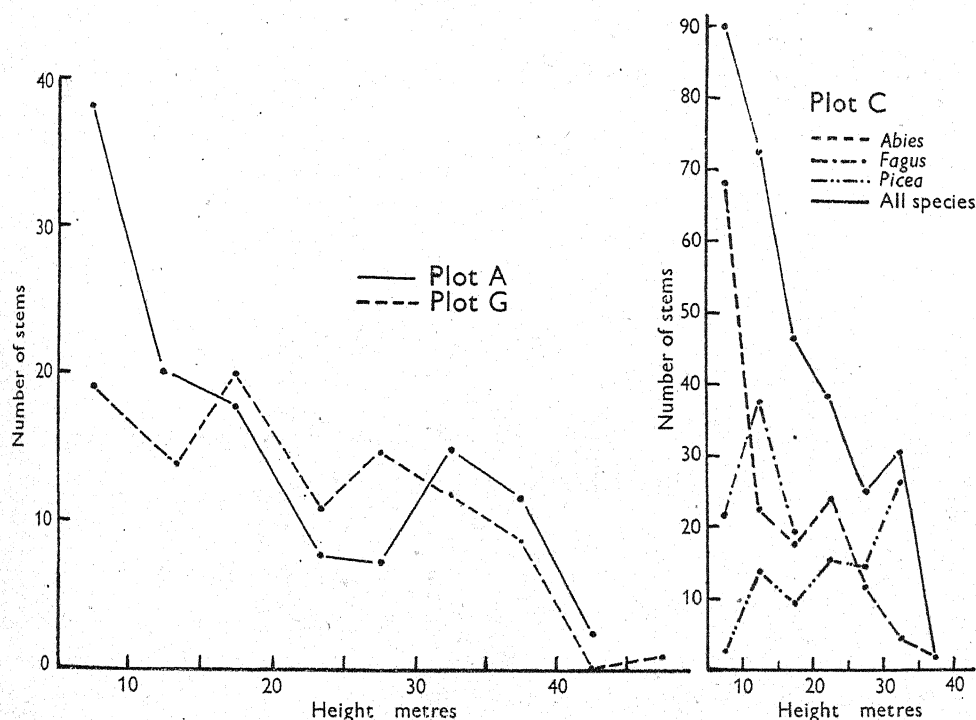
Fig. 2. Height distributions of stems in three of Mauve's sample plots in the Carpathians. Plot A. Mature *Abies-Picea-Fagus* forest with continuous canopy and 'storied' structure. Plot C. Young forest of similar character. Curve based on measurements of a 10% sample. Plot G. Pure *Picea* forest with irregular 'selection forest' structure on rocky ground. Note that the curve for A shows a distinctly two-storied structure, a feature consistently shown by the other plots in this type of forest; there is no such tendency in G. In plot C *Picea* was apparently the pioneer and forms an overstory, *Fagus* and *Abies* being generally smaller, but stories are not sharply defined.

distributions resembled those for all-aged 'selection' forest except for a deficiency of the smallest sizes (plot A, Fig. 3). Age determinations on two of the plots show, however, that for individual species the ages were by no means regularly distributed (Fig. 4). Thus on plot A 26% of the *Fagus* were from 20 to 70 years old, 10% were from 80 to 180, and 37% were from 240 to 270 years old. In plot B, 47% of the *Abies* were 40–100 years old, 53% 200–300 years old, with none between the ages of 100 and 200; during this period there had been entry of *Fagus* and *Picea*.

Two further plots were in relatively young crops of limited extent, containing no trees older than 100 and 130 years in plots C and D respectively; they clearly represent seral
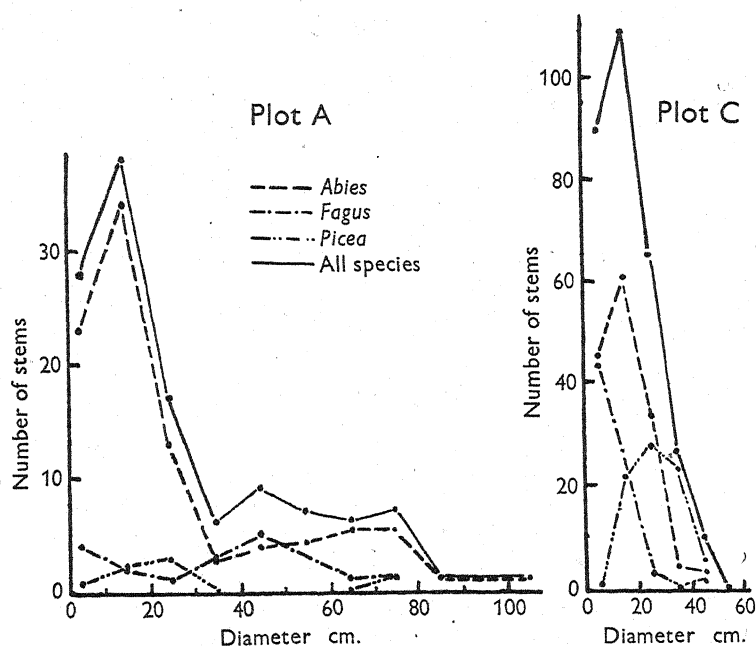
Fig. 3. Diameter distributions in two of Mauve's sample plots. See Fig. 2. The curves suggest that in A there are two age groups for each of the three species, the present phase being one of entrance of *Fagus*; in C there appear to have been waves of entry of *Picea* and *Abies* and, most recently, of *Fagus*.
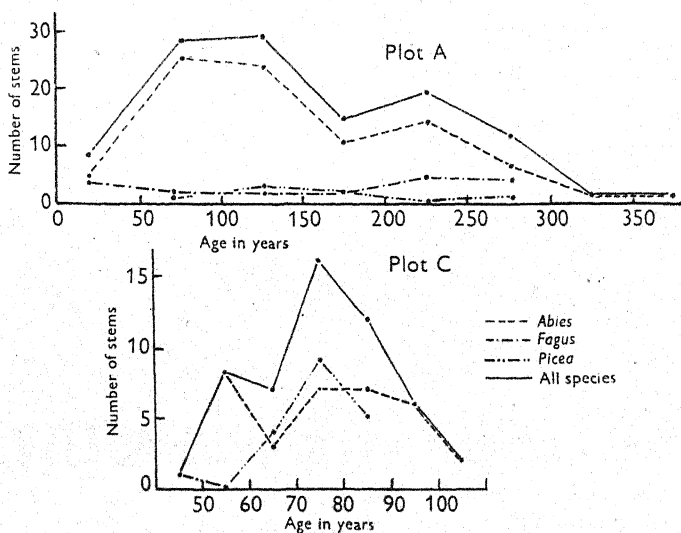
Fig. 4. Distribution of ages in two of Mauve's plots. See Figs. 2 and 3. In A the curves are closely related to those for diameter distribution, the same maxima and minima being traceable in each. In plot C *Fagus* was not sampled, and the curves for *Picea* and *Abies* are based on a 20 % sample; this probably explains the discrepancy between this and the evidence given by diameters and heights respecting the order of entry of *Picea* and *Abies*. Figs. 2-4 after Mauve (1931).

stages in the development of the more widespread condition. These two stands had the general appearance of even-aged crops, even though there was an age range of 50 years among the dominants, and the stands as a whole were all-aged. Plot D had a canopy of 100–130-year-old *Picea*, with younger *Abies*, which had entered in two waves, forming an understorey. This plot was on a more degraded soil than plots A, B, C, E and F, and this fact may perhaps account for the absence of beech. Plot C is particularly interesting; the height and diameter distributions (Figs. 2, 3) make it clear that as in plot D *Picea* was the pioneer species, and that, though some of the *Abies* was as old or older than the oldest *Picea*, it was in general a later arrival, while the immigration of beech began still more recently, and was still in progress. Beech was also the principal species regenerating in plots A and B, which represent a stage some 200 years later than C; one may therefore speculate as to whether plot F, which had a light stocking of very large-crowned beech,
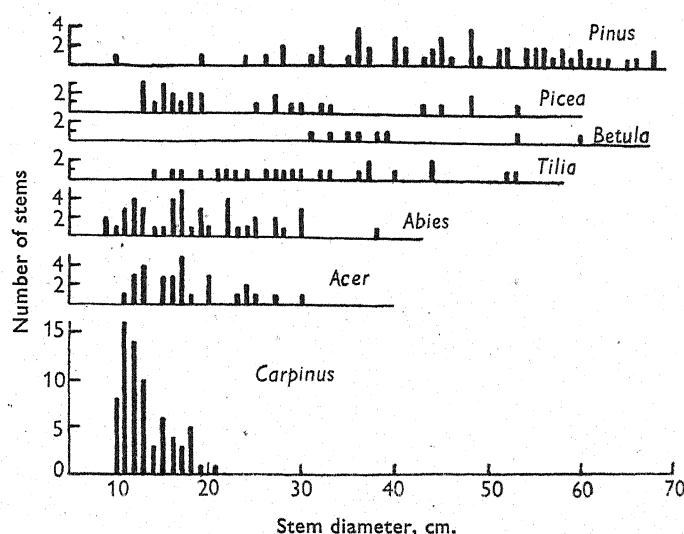
Fig. 5. Diameter distributions of the principal species in Iwaschkewitsch's plot in Manchuria. Note the indication of strongly periodic entry of *Picea ajanensis*, and suggestions of this in *Pinus koraiensis* and *Abies nephrolepis*. A more or less even-aged condition is indicated in the case of *Carpinus cordata* and possibly *Acer pseudo-sieboldianum*. Modified from Iwaschkewitsch (1929).

represents a rarely attained end stage, or whether this merely represents a local variant due to chance or to site conditions.

Iwaschkewitsch gives exceptionally full details for a sample plot in forest of more complex composition in the Usuri district of Manchuria. A selection of his figures are given in Table 1 and Fig. 5. *Pinus koraiensis* was the principal dominant species, but though there was abundant suppressed regeneration less than 0·5 m. tall of this species, the enumeration figures (cf. Fig. 5) make it clear that it has certainly made no continuous entry into the canopy, where the youngest trees were 147 years old. The smaller trees in the lower height classes represent, not young trees about to enter the upper canopy, but feeble individuals which are being suppressed but are of the same ages as those in the main canopy. In the case of *Picea ajanensis* the various height classes do represent different age classes; the diameter frequencies show that it has entered in the past in two sharply separated waves, while a third wave had just entered, or perhaps was still entering, despite

10-2

the small proportion of this species in the regeneration. The remaining important species were definitely confined to the lower stories; the age determinations and the absence of dead stems show them all to have been relatively recent entrants, *Acer* sp. and *Carpinus cordatus* being the most recent, and the stem-diameter frequencies suggest in each case a restricted period of entry.

Table 1. *Composition of 0·4 ha. of Virgin Forest in the Usuri district, Manchuria. Modified from Iwaschkewitsch (1929a)*

Species	Height class	Number of stems		Volume of timber			Dead as % of living	Ages of sample trees (yr.)	% of regeneration
		Total	Rotten	Total	Rotten	Dead			
Pinus koraiensis Sieb. & Zuc.	1	30	11	78·0	32·7	3·9	5·1	196, 218, 226, 227, 238, 246	18
	2	18	9	34·7	18·3	6·8	19·6	167, 230, 249	
	3	6	1	4·4	0·5	0·7	15·8	142, 213	
	4	4	3	1·4	1·4	1·5	107·0	170, 212, 240	
	Total	58	24	118·5	52·9	12·9			
Picea ajanensis Fisch.	1	2	1	4·3	2·3	4·2	98·0	160, 200	5
	2	4	1	6·8	2·4	0	0	135	
	3	4	1	2·4	0·4	0·9	36·8	130	
	4	18	4	2·7	0·4	0·6	22·7	73	
	Total	28	7	16·2	5·5	5·7			
Betula costata Trautv. & Mey.	1	6	2	9·4	2·5	0	0	170	
	2	2	1	2·8	1·0	0	0	107	
	Total	8	3	12·2	3·5	0	0		
Tilia amurensis Kom.	2	6	1	10·2	2·5	0	0	110, 118, 159	12
	3	5	1	3·1	0·4	0	0	86	
	4	11	3	4·4	1·5	0	0		
	Total	22	5	17·7	4·4	0	0		
Abies nephrolepis Max.	2	1	1	1·1	1·1	0	0	124	2
	3	8	3	3·7	1·4	0	0	84, 132	
	4	42	14	6·1	2·4	0·92	14·8	104, 121	
	Total	51	18	10·9	4·9	0·92			
Acer pseudo-sieboldianum Komar.	3	3	0	1·5	0	0	0	132	19
	4	26	0	2·8	0	0	0	113	
	Total	29	0	4·3	0	0	0		
Carpinus cordata Bl.	4	69	0	6·6	0	0		74, 82	18

In addition to the trees listed above there were 3 stems of *Fraxinus manschurica* Rupr., 3 stems of *Ulmus montana*, one stem each of *Quercus mongolica* Fisch. and *Micromeles (Sorbus) alnifolia* Koehne and an understorey of shrubby species.

Height classes: 1 24–29 metres
2 20–24 metres
3 16–20 metres
4 Less than 16 metres

The regeneration consists of plants less than 0·5 metre tall, of which there were 57,500 per ha.

DEATH AND REGENERATION

The even-aged condition and the role of fire

The even-aged condition implies widespread destruction followed by complete regeneration within a limited period of time. Fire has generally been regarded as the principal destroyer, and several authors, e.g. Müller (1929), have assigned it a role of supreme importance in the natural forest. Doubtless even-aged stands often have originated after fires, and fires have occurred from the very earliest times, as is shown by layers of charcoal in peat, and by ancient fire scars occluded in trunks; one has been found on *Sequoia* dating from A.D. 245 (Show & Kotok, 1924). Keen (1937) records a 670-year-old tree in eastern Oregon which had been burned twenty-five times between 1481 and the present day. Huberman (1935) and Hough & Forbes (1943) give other examples of early burnings. There has, however, been much dispute as to the extent to which fire must be considered a natural as opposed to a man-made occurrence. Lightning is the principal natural cause of fire, though there is at least one well-authenticated case of fire caused by sparks from a boulder crashing down a stony slope (Moir, 1923). Authenticated details of the beginning of several forest fires started by lightning are also given in Moir's note. Most fire statistics give the percentage of fires due to various causes, and, since this figure depends very largely on the density of population of the country, are useless for the present purpose. It has been possible, however, to obtain some figures on the basis of number of fires per annum per unit area of forest. In northern Finland 4·13 fires per annum per 100,000 ha. of forest are ascribed to lightning, and in southern Finland 9·28 (Saari, 1923). In fires per annum per 100,000 acres of forest, the form in which the following American data will be given, these figures are 1·67 and 3·76 respectively. American statistics show that over most of the United States the lightning fire hazard is rarely more than 0·126 fire per 100,000 acres, and often much less, e.g. 0·04 in Minnesota (Mitchell, 1927). But there are limited areas with a far higher incidence of lightning fires, e.g. the Northern Rockies, with 3·72 per 100,000 acres. The average figure for California as a whole is 2·94, but over those parts of the State where lightning is an important cause of forest fire it is 4·03, rising locally to 6·15 (Show & Kotok, 1923). Keränen (1927) concludes that the number of fires ascribed to lightning in the Finnish statistics is too great. He points out that in the north, between latitudes 64 and 70° N., the number of days per year with lightning averages only six to eight, and not more than half the fires attributed to that cause were on days when, from meteorological data, lightning seemed likely. However, there were certain days when weather conditions were eminently suitable for lightning storms, during which abnormally large numbers of fires occurred, e.g. in northern Finland on 9 July 1925, thirty fires were reported. On the basis of this evidence Keränen agrees that lightning is undoubtedly one of the most important causes of forest fire in northern Finland. He states that on suitable days the storms often seem to cling to wooded areas, and there is often much lightning with little rain. In America, too, the same feature is conspicuous; suitable days may be rare, but when they occur numerous fires are started. In California up to 350 fires have been started on a single day by a single storm as it travelled over the country (Show & Kotok, 1923), and it is not uncommon for over 200 fires to start from a single storm. Thus one must conclude that while there are large areas where lightning is a negligible cause of fire, there are restricted areas where it is a most

important factor; in such areas the even-aged stand following fire must be the primeval condition.

Even-aged stands or components of stands can certainly originate in other ways however, and even in North America where the frequency and importance of fire is undoubtedly great, some authors have suggested that its importance has been greatly exaggerated. Raup (1937) has put forward this case with much and varied evidence, suggesting that the apparent replacement of *Pinus strobus* in the Lake States and, farther south, of *Quercus* and *Castanea* spp. by the more tolerant species of *Fagus*, *Acer*, *Tsuga*, etc., may be due to a readjustment of the dominants following climatic changes rather than to a succession following fire.

Wind-throw, when it occurs on sufficient scale, can originate even-aged stands. Hough & Forbes (1943) illustrate a case where *Pinus strobus* had originated in this way, the seedlings germinating on the mounds of soil made by the upturned roots of the old stand; the mature *strobus* consequently had extraordinary stilt-like roots. However, it does not seem to be an important originator of seres except perhaps in the arctic, where Nichols (1935) says that it is common over great areas.

Graham (1941 b) describes a part of the Ottawa National Forest in Michigan which has had no fire for some centuries. Between the years 1875 and 1938 there had been no regeneration of *Tsuga canadensis*, but during the period 1938–41 there was very free regeneration; this he attributed to a succession of moist summers. Hough & Forbes also comment on the periodic reproduction of *Tsuga*. Irregular seed production can also contribute towards the even-aged condition; even species which fruit frequently produce exceptional crops of seed at more distant intervals, and it is the general experience of foresters that only these exceptional crops are likely to cause any appreciable extension of the species in the stand.

Periods of climatic stress can help to bring about the death of large numbers of old trees within a short space of time; Hough & Forbes say that drought such as that of 1929–30 in eastern United States 'results in heavy mortality among shallow-rooted species such as *Betula lutea* and *Tsuga canadensis*, particularly on shallow soils', and 'observations during the drought of 1930 and more recently in East Tionesta show that the result is in mortality of larger or overstory trees of hemlock'.

Inundation or draining of lowland tracts through the activity of beavers can be an important form of catastrophe (Gates, 1942). Even-aged stands can originate following retreat of glaciers, e.g. in Alaska (Cooper, 1942), and on a smaller scale in the European Alps. Cycles in mammalian populations may well be important in determining periods of regeneration, though so far as I am aware this has never been demonstrated.

It seems likely that once an even-aged stand has been established, it may persist through several generations, irregularity only being attained very gradually as the age range of successive generations becomes greater, and through the cumulative effect of accidents such as wind-break. The successive generations need not be of the same species. Müller, as a result of his work in the Balkans, suggested that some such sequence of even-aged stands of different species, always ending in catastrophic destruction, usually by fire, was the usual condition in virgin forest. There is no doubt that his views are much too extreme; moreover, he appears to have been very uncritical in his selection of examples of 'Urwald'. There is, however, probably some truth in this idea of a sequence of more or less even-aged crops. The young even-aged stand excludes regeneration by its density.

As it ages, the first gaps which are formed will be quickly closed by the lateral expansion of surrounding trees, any regeneration which may have entered them being suppressed, so that the stand would remain even-aged until it was composed of large old trees, many of which would be nearing the end of their normal span of life together. Once permanent gaps began to form as a result of the death of the first of these old giants, the end of the remainder would be hastened by sun-scorch on the exposed trunks and by the die-back of the crown which always seems to affect old trees which have been isolated after having grown in closed stand. Thus an old stand might break up and die, admitting regeneration for the first time, within a period which was short in comparison with its life. Several authors believe that this kind of process does occur. Willgerodt (in Gerhardt, 1923) (Carpathians) and Cermak (Balkans) apparently believed that this happened. Hesmer (1930) records old stands of *Pinus leucodermis* and *P. peuke* Griseb. which he believed were breaking up in this way, and Iwaschkewitsch pictures some process of this kind for the regeneration of his Manchurian forest. 'Observations on the age of regeneration in various places in the district and the study of cross-sections of old trees which have survived a period of suppression in their youth, agree in showing that in our pine forests the closure (of the canopy) remains uniform during a period of 35–40 years, and then decreases as the result of high mortality of trees. At this moment considerable regeneration arises, and suppressed advance growth begins to grow. The subsequent increase of the closure as a result of the growing up into the canopy of the formerly suppressed trees culminates in about the same length of time, and then the process begins anew' (Iwaschkewitsch, 1929 *a*, p. 139). There seems no doubt that it happens with the short-lived intolerant species (e.g. *Populus* spp. (Müller, Zednik), *Alnus* spp., *Prunus* spp., *Betula* spp. (Schenck, 1924), etc.) which are so often the pioneers after catastrophes.

THE DEATH OF TREES IN THE VIRGIN FOREST

There have been few studies of the relative importance of various causes of death in virgin forest. Apart from violent death by tempest and fire, possible causes such as root- or heart-rot and attack by insects and fungi are perhaps better regarded merely as phases of senescence and contributory causes to natural death by old age or suppression. Many writers emphasize the very large amounts of dead wood which are commonly present at all stages of development. In stands such as Mauve's 60–100-year-old *Picea-Abies-Fagus* elimination by suppression of the smaller stems is in progress. But in many, perhaps most, virgin stands many of the larger trees are heart-rotten, and there is much standing and fallen dead timber of large size. Lutz (1930, *Tsuga-Fagus-Acer-Pinus strobus* in Pennsylvania) records about a twelfth of the total basal area* as being formed by dead standing timber. At Kubany the volume of dead timber, standing and fallen, equals that of the living. Mauve and Fröhlich emphasize the abundance of scattered fallen stems of large size, and Markgraf's plot shows the same feature. In these cases the old trees have obviously died and fallen one by one; the catastrophic creation of large gaps by wind, etc., is exceptional. Korstian (1924) records the death in a period of five years in a *Pinus monticola* stand (Idaho) of 137·5 cu.ft./acre (9·6 cu.m./ha.); this was 3·3 % of the total volume of timber, and was almost entirely composed of the largest trees. The mean annual increment (i.e. new wood actually formed per year) was 55·5 cu.ft./acre (3·85 cu.m./ha.),

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* Cross-sectional area of trunks at height of 4 ft. 6 in.

but in some parts of the stand there was actually a decrease in total volume over the period, the volume of trees dying being greater than the increment on the living trees. If death at this rate continued over a long period, all the dominants would have died in the space of 50 years. This stand might well be breaking up in the way which has just been suggested in the previous section. Insects (mainly bark-beetles) were stated to be responsible for two-thirds by volume—about a half by numbers of stems—of the deaths. Windfall was the second most serious cause of death. Korstian gives no information on what was replacing the pine.

Clearly, then, in a wide range of forests, including that of the tolerant species of Europe, death by old age is usual, and catastrophes, whether major or minor, unimportant. Clearly, too, there is often casual death of isolated trees such as might lead to the development of all-aged structure.

REGENERATION

An enumeration of stems' ages and sizes, when sufficiently complete, gives a good indication of the past course of regeneration. It is more difficult to say what species are actually entering a stand at the time. Very often the species regenerating appear to differ, at least quantitatively, from those forming the stand. The universal predominance of beech seedlings, even when there was little in the crop, made Mauve suggest that succession was still in progress. Cain (1935) instances the abundance of seedlings of *Acer saccharum* Marsh. and *Ulmus americana* L. in stands where *Fagus grandifolia* Ehrh. was the dominant, and *Ulmus* very subsidiary. But relative abundance of seedlings is not a safe guide, since seedlings which are failing to establish themselves may yet be very abundant. In the Manchurian *Pinus koraiensis* forest seedlings of *Pinus* formed 18% of the regeneration, those of *Picea ajanensis* only 5%, though the former was not entering the crop while the latter was.

There are, however, many instances cited where seedlings of one or more species of the mature stand are completely absent, e.g. *Pinus strobus* (Graham, 1941 a; Lutz, 1930, etc.), *Quercus alba* L. (Lutz). Schenck (1924) goes so far as to say that he has never seen a pure stand regenerating with the same species except after fire, and that he has never seen regeneration of *Castanea*, *Carya* or *Quercus* spp. (except *Q. coccinea* Muench. on one occasion) in the North American virgin forest. There is a very strong belief amongst Continental foresters in the tendency of one species to regenerate beneath the canopy of another species, at least in the case of certain pairs of species such as *Abies alba* and *Picea abies*.

A striking feature of regeneration in the virgin forest which has often been commented on is the abundance of seedlings on rotting logs and stumps. Only a limited number of species have the ability of growing on this substratum, e.g. *Picea* spp. in Europe and America, *Tsuga*, *Thuja* and *Betula lutea* Michx. in America.

DISCUSSION

Virgin forest and the theory of the climax

Ecological theory postulates that climax vegetation is in dynamic equilibrium with its environment; individuals may die and their place be taken by individuals of other species, but compensating changes take place elsewhere, and the community as a whole remains

unchanged. To the forest, which is perhaps the most widespread and most complex type of climax vegetation, we must look for evidence as to the extent to which this condition is attained. It is conceivable that 'climax forest' is a concept only, never existing in practice either because of catastrophic initiation of fresh seres, or because of the time lag —necessarily great where long-lived trees are concerned—in the adjustment of the vegetation cover to an ever-changing environment. Even if the climax condition is attained, theoretical considerations give us no clue to what might be called its 'minimal area'—the extent of the area within which the kaleidoscopic vegetation pattern remains unchanged in the aggregate, nor do they indicate the degree of precision with which the climax could be defined. There might, for example, be several variants which were equally stable and capable of replacing each other in time or space.

The facts relating to the structure and reproduction of the forest can now be surveyed from this point of view. In the first place it must be noted that most of the evidence relates to forests of tolerant ('shade-bearing') genera such as *Fagus*, *Acer*, *Abies* and *Tsuga* spp., which are undoubtedly the ultimate dominants in mesic sites with adequate rain. The status of intolerant ('light-demanding') genera such as *Pinus*, *Larix*, *Quercus* and *Castanea* is less clear. They certainly often form early seral stages to forest of tolerant species, but may remain permanently dominant in the far north, at high altitudes and on barren soils in more temperate regions, and in warmer, more arid climates. We have seen that mass regeneration following catastrophe may be usual in the Arctic. The alpine forest has scarcely been studied from the point of view of structure, but it often has extreme irregularity imposed upon it by a broken terrain and violent climate, or else is heavily grazed. The remaining categories of forest of intolerant species are all particularly open to human interference. They are mostly found in populous regions under warm dry conditions. In contrast to the 'tolerant' forest they burn easily, and in consequence, frequently are burned, either accidentally, or by herdsmen. Markgraf stresses the contrasts between the beech forest of the Balkans, difficult to burn, with little fodder in its deep shade, and therefore undisturbed, and the adjacent inflammable pine and oak forest in the lower zone, with abundant grazing beneath its light canopy, and therefore regularly burned. It is probably impossible to say to what extent intolerant species would be replaced by tolerant species if fire were completely excluded, as has been the case with *Shorea robusta* in parts of India and some of the thorn scrub forests of west Africa. In any case, we cannot look to them for evidence on the structure and behaviour of climax forest.

We have seen that as a general rule in 'tolerant' forests catastrophes are rare and of small extent, single trees or at most small groups being thrown by wind, etc. There will, then, be a forest in which intolerant species will only get an occasional footing in the larger gaps, and since in any one region the available number of tolerant species which are potential dominants on account of size, longevity, etc., is not great, there must be some degree of constancy in specific composition. The difficulty of deciding whether the existing structure and proportions of species are being maintained must be emphasized once more. A detailed study of the sizes and ages of very representative samples of the stems on a plot of considerable size is practically essential. In irregular forest of 'selection' structure it is obvious from the abundance and intimate mixture of stems of all ages that the existing structure is being maintained, but, as we have seen, this is of restricted occurrence.

The more usual type of forest where there is a wide range of ages has a continuous uniform canopy, often with much the aspect of an even-aged crop, but often with a more or less pronounced storied structure. A number of plots of this kind of forest have been described where it is possible that the existing condition is being perpetuated, but full proof is lacking, either because of inadequacy of the enumerations, small size of plot, or some other deficiency in the data. These examples are not numerous however; e.g. in only one plot (7*b*, pure beech) out of twelve for which Fröhlich gives figures does this condition appear likely. We have seen that some degree of differentiation of discrete age classes seems usual, and this itself implies periodical reproduction of a species and fluctuating composition and structure. Mauve's and Iwaschkewitsch's plots are of special value on account of their very full enumerations and age determinations, and in all these except one (Mauve's plot G—'selection structure' spruce) it is obvious that composition is fluctuating, at least on the limited areas of the plots (0·25 ha. for Mauve and 0·4 ha. for Iwaschkewitsch). This is particularly the case with the Manchurian plot, with its more complex mixture of species than is usual in Europe. The average composition might of course remain unchanged over a sufficiently large extent of uniform site.

But in a mixed stand there will almost certainly be species differing from each other in their natural span of life, the periodicity of their seed years, the exact conditions of site and climate needed for the establishment of regeneration, and other biological traits. Climate itself undergoes cyclical changes quite apart from any secular trends, and a generation of trees initiated by a favourable period in the cycle will persist through many succeeding cycles, and when conditions become ripe for regeneration once more it might well be for regeneration by a different species and at a different phase in the cycle. It would not, then, be surprising if the entry of any one species in sufficient quantity to form an important constituent of a stand occurred only at distant intervals of time, as the result of some rare combination of circumstances. Thus a forest which is ever varying in the proportions of its species would arise. On a mountain side in central Europe beech might be dominant for a generation, to be followed in one place by a preponderance of silver fir, in another place perhaps by a preponderance of spruce. The many communities of varying specific composition which can so often replace each other on the same site as the result of some slight disturbance of balance, may then have equal claim to be considered as part of the climax, and the climax itself would be a mosaic of communities, at least in time, and possibly in space also. This is the kind of picture which seems to be suggested, however vaguely, if the temperate forests which have been accepted as 'virgin' are in fact the product of immense periods of growth undisturbed by catastrophes or by extraneous interference. Other students of forest vegetation have been led, on various grounds, to make suggestions which are akin to this. Nichols (1935) writes: 'The climatic climax...is most useful when interpreted broadly, to embrace a series of plant associations which may vary more or less widely among themselves in floristic composition and to some extent also in ecological structure. Thus in the Eastern Hemlock region there is no one plant association which stands out, to the exclusion of other associations as being the climatic climax.' Graham (1941*a*) wonders whether the stable climax is not like 'a phantom, always moving ahead into the future, and becoming visible for only relatively brief periods on small areas...', and whether ecologists should not avoid 'the assumption that culmination in an ultimate climax is the necessary or even the end result' of succession. Whether suggestions of this kind are correct or not only further study of presumed

examples of virgin forest can show, but I have endeavoured to demonstrate that at least a very strong case can be made out for them, and that the generally accepted concept of the climax may need considerable modification in detail to fit the temperate forest. For the rest, I have tried to review the information available on certain aspects of a rather nebulous and ill-defined subject which have interested me and which may prove of value to others.

Note. An important recent American contribution by Cline & Spurr (1942) only became available while this Review was in the press; it does not necessitate any modification of the statements made. Unfortunately, it is impossible to reconstruct accurately the original figures for numbers of trees per plot from the summary of percentage composition given in the appendix. The importance of the paper lies in the attempt to separate climax from seral phases, and to show the influence of topographical position on the climax. In the plots where there was no trace of past disturbance, and which therefore presumably represented the climax, it seems likely that the existing composition was being perpetuated, except where *Pinus strobus* was concerned.

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MORPHOLOGY OF THE VEGETATIVE SHOOT IN EPACRIDACEAE

By K. J. DORMER

Botany Department, Queen Mary College, University of London

(With 6 figures in the text)

According to Sinnott (1914), the Epacridaceae are characterized by the possession of multilacunar nodes, and differ in this respect from all other Ericales, the Clethraceae, Pyrolaceae, Ericaceae, and Diapensiaceae being constantly unilacunar. Bailey & Sinnott (1914) quote the family as an example of the association of sheathing leaf-bases with multilacunar nodes. As Hasselberg (1937) has pointed out, the work of these authors loses much of its value by their failure to give the names of the genera and species which they examined. On referring to the account given by Drude (1889), it appears that sheathing leaf-bases occur in only five out of twenty-one genera. The habit of the majority of the family is thoroughly ericoid, which would lead one to expect that the nodes would be unilacunar. I am indebted to Mr R. H. Richens for the information that he had personally observed *Epacris ardentissima* and *Styphelia richei* to be unilacunar.

In view of the obvious desirability of a more extensive investigation, material was obtained representing twenty-one species belonging to fifteen genera. In this material it has been possible to distinguish three clearly defined types of leaf-base.

Typical unilacunar nodes, with narrow leaf-bases, the leaf-scar occupying, at most, about a third of the circumference of the stem, are found in *Lebetanthus americanus*, *Lysinema pungens*, *Epacris impressa*, *Styphelia triflora*, *S. adscendens*, *S. distans*, *S. parvifolia*, *S. acerosa*, *Monotoca lineata*, *Acrotriche serrulata*, *Brachyloma* sp., *Pentachondra involucrata*, *Trochocarpa thymifolia*, *Needhamia pumilio*, and *Oligarrhena micrantha*. A shoot of this type is shown in Fig. 1, which represents a species of *Styphelia*. The same type of structure may be expected to occur also in the genera *Prionotes*, *Woollsia*, *Archeria*, and *Conostephium*.

In *Cosmelia rubra* (Fig. 2), *Sprengelia aristata*, and *S. incarnata*, the base of the leaf embraces the stem, the width of the insertion being actually greater than the circumference of the stem, so that the edges of the leaf-sheath overlap, as in many monocotyledon (Fig. 4). In view of this arrangement it is rather surprising to find only a single foliar trace. Immediately above its point of entry into the leaf, this bundle gives off two branches which run almost horizontally round the base of the sheath. From these girdling bundles spring a number of smaller strands which together form the parallel venation of the leaf sheath and limb.

The leaves in these two genera are shed in a very peculiar manner. Separation takes place in the region of the pericycle, so as to cast off not only the leaf but also the entire cortex of the internode below. At this stage the leaf, with its attached frill of stem cortex, can be slipped freely up and down the stem. Owing to the rigidity of the overlapping sheath a leaf may remain in this condition for some time, but a slight lateral pull will suffice to remove it. The collar of stem-cortex is relatively flimsy, and breaks at a touch,

whereupon the sheath opens, the stem slips out of it, and the sheath, which is tough and elastic, returns to its original form. Fig. 5 represents diagrammatically a sheath which has been flattened out, the vascular system being shown in black. The part below the point of origin of the leaf trace is stem cortex, the part above is leaf-sheath. When the leaves are gone the stem is left stripped to its pericycle. There are no 'leaf-scars' in the accepted sense of the term, the only markings being vertically elongated depressions
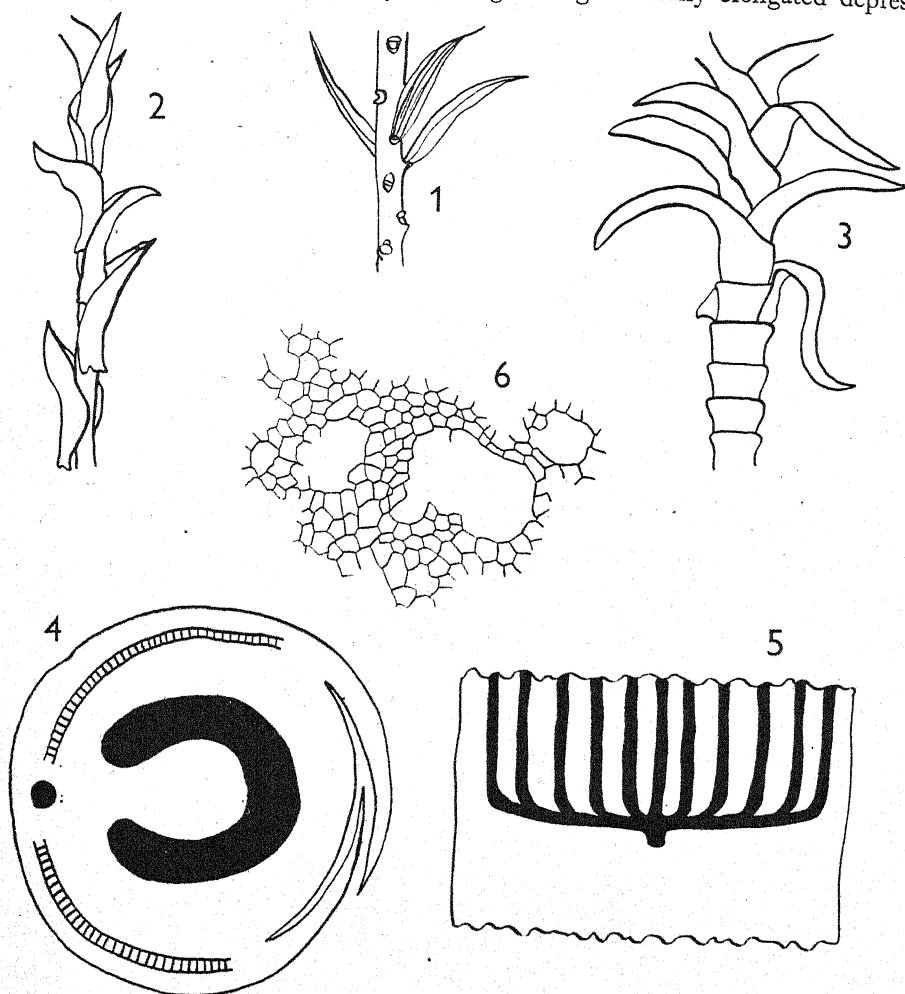
Figs. 1–6. 1, shoot of *Styphelia* sp. 2, shoot of *Cosmelia rubra*. 3, shoot of *Richea gunnii*. 4, transverse section through a node of *Cosmelia*: xylem cut transversely is black, that cut longitudinally is cross-hatched. 5, diagram of a leaf-base of *Cosmelia* flattened out: vascular system black. 6, pith of *Richea dracophylla* in transverse section, × 75.

indicating the positions of the foliar gaps. It is not definitely known whether this remarkable process has any close relation to the formation of periderm, but such a relationship seems highly probable. These shoots are perhaps of some interest in connection with the leaf-skin theory (Saunders, 1922).

In *Dracophyllum longifolium*, *Richea dracophylla*, and *R. sprengelioides* the leaves have overlapping sheaths, but the vascular supply is quite different from that of *Sprengelia*

and *Cosmelia*. Besides the median foliar trace there are a number of lateral traces. The exact determination of the number of traces is a matter of some difficulty, as they pass out very abruptly and at different levels, so that it is never possible to see all the traces of a leaf in a single section. Apparently in *Richea sprengelioides* there are constantly three traces, one median and two lateral, the insertion occupying about two-fifths of the circumference, so that the lateral traces of successive leaves are roughly superposed. In *Richea dracophylla* and *Dracophyllum longifolium* there are more than three traces, and they are spaced out round the whole circumference. The traces in these genera run straight out into the leaf sheath, and there are no girdling bundles like those of *Sprengelia* and *Cosmelia*. The leaves separate from the stem in a normal manner, leaving ring-shaped scars, and the stem cortex remains intact (Fig. 3). The same type of structure may be expected to occur in *Sphenotoma*.

Taxonomically, these results are of interest in that they tend to emphasize the distinctness of *Dracophyllum* and *Richea* from the rest of the family. In view of the peculiar mode of leaf-abscission in *Cosmelia* and *Sprengelia* it is difficult to regard these genera as being in any sense intermediate between the *Dracophyllum* group and the forms with ericoid shoots. In this connexion the histology of the pith seems to be of importance. In all the unilacunar species examined, including *Sprengelia* and *Cosmelia*, there is a quite ordinary, solid, parenchymatous pith, the cells being of more or less uniform size, though with a tendency to be smaller towards the edges, and with walls of uniform thickness. In *Richea dracophylla* and *Dracophyllum*, however, there are, intermingled with the ordinary pith cells, much larger elements with thin walls, giving the pith as seen in transverse section a highly characteristic spongy appearance. In some cases these enlarged cells break down to leave large irregular cavities, as seen in Fig. 6. As only herbarium material has been available, nothing is known as to the origin or function of this structure. There is little doubt, however, that in this family an important distinction may be drawn between the genera with solid pith and no lateral traces and those with lateral traces and a spongy pith. The existing classification fails to make this distinction, and groups together all the forms with sheathing leaf-bases (Drude, 1889).

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A SUBMERGED PEAT BED IN PORTSMOUTH HARBOUR.
DATA FOR THE STUDY OF POST-GLACIAL HISTORY. IX

By H. GODWIN

Botany School, Cambridge

(With 1 figure in the text)

In the summer of 1943, through the courtesy of Mr A. W. Skempton of the Building Research Station of the Department of Scientific and Industrial Research, I was sent a sample of peat obtained from a level of − 59 ft., O.D., near the Weevil Lake, Gosport, in Portsmouth Harbour. The stratigraphy was as follows:

> ft. O.D.
> 0 to − 7   black silt and stones
> − 7 to − 54   blue organic silty clay
> − 54 to − 60   peat and peaty clay
> − 60   flint pebbles

TREATMENT

Seeds and fruits were extracted for the most part by treating the peat with dilute nitric acid in the cold for 24 hr. or more, and then washing and sieving.

Samples were prepared for pollen analysis in accordance with the following scheme of treatment:

(a) Digest about 1 c.c. of the moist peat for 1–2 hr. at 100° C. with 10% NaOH, strain to remove debris, fruits, seeds, etc., centrifuge at 2000–3000 r.p.m. for 3–5 min., decant the liquid, stir up the centrifugate in distilled water, and recentrifuge.

(b) Stir up the centrifugate in 8 c.c. glacial acetic acid + 4·5 c.c. $NaClO_3$ solution (one part by weight in two of water) + 1 c.c. conc. H_2SO_4, and leave in the cold for several hours. Dilute, centrifuge and wash thrice as in (a).

(c) Stir up the centrifugate with 10 c.c. glacial acetic acid + 1 c.c. conc. H_2SO_4, and keep at 100° C. for 20 min. Dilute, centrifuge and wash thrice as in (a).

(d) Transfer the centrifugate to a platinum crucible with 3–5 c.c. conc. HF and heat to boiling for 2 min. in an efficient fume cupboard. Stir the mixture into 5% HCl, centrifuge and wash twice as in (a).

(e) Transfer the centrifugate to a boiling-tube and dilute with twice its volume of hot safranin glycerin jelly. After thorough mixing make five slides, employing a warmed pipette to get an even spread of jelly, enough to extend to the full area of a large cover-slip.

POLLEN COUNT

The recorded tree-pollen percentages on a count of 150 grains are *Betula* 61%, *Pinus* 24%, *Quercus* 15%, *Alnus* +. Not reckoned in the total tree-pollen, but expressed as a percentage of this figure are also 3% *Corylus* and 47% *Salix* pollen.

The non-tree-pollen includes 115 % grass, 33 % *Carex*, and occasional grains of *Typha*, *Taraxacum*, *Ranunculus*, *Galium*, and *Myriophyllum alterniflorum*, the last-named a type highly characteristic of late-glacial and pre-boreal layers throughout north-western Europe. There are also 45 % fern spores.

SEEDS, FRUITS, AND WOOD

Ranunculus flammula L. Seven achenes (Fig. 1, *t, u*) characteristically pitted. Though of the size and shape of the achenes of *R. flammula* there is no means of being certain that they may not be *R. reptans* or *R. scoticus*.

Potentilla palustris L. Ten achenes.

Menyanthes trifoliata L. Some 80–90 whole and half-seeds.

Lycopus europaeus L. Twenty-nine nutlets, mostly with the characteristic inflated border, but others without (Fig. 1, *x, y, z*).

Urtica dioica L. Two half-fruits (Fig. 1, *v*).

Betula verrucosa Ehrh. One intact female cone-scale (Fig. 1, *a*), about forty fruits all without wings: most or all of these accord in size and shape with *B. verrucosa* but means for exact diagnosis are lacking (Fig. 1, *b, c*).

Betula nana L. Four fruits (Fig. 1, *f–i*). The smallest of these (1·0 × 0·6 mm.) has one intact wing. The other three are without but in size and shape agree with *B. nana*, though possibly the two largest could be referred to the next-mentioned hybrid.

Betula nana × pubescens. One intact female cone-scale (Fig. 1, *d*) appears likely to belong to this hybrid. This scale is quite unlike those of *B. verrucosa*, *B. pubescens*, or *B. nana*, and corresponds closely with some, though not all, of those from the cones of the hybrid *B. intermedia* Gürcke, which is recorded in Britain from a limited region of Scotland. Female cone-scales attributed to the hybrid *B. nana × pubescens* have been recorded by Jessen & Milthers (1928), from Herning and other sites in Jutland and north-west Germany, out of the last interglacial. One fruit (Fig. 1, *e*) may perhaps be referable to this hybrid also.

Salix. One piece of wood identifiable microscopically.

Scirpus fluitans L. 1 nutlet (Fig. 1, *w*).

Scirpus lacustris L. Ten fruits which appear to include a wide variation in proportion of length to breadth, but not more than the range of recent material (Fig. 1, *p, q, r*).

Carex disticha Huds. Two nutlets (Fig. 1, *m, n*).

C. goodenowii Gay. One nutlet (Fig. 1, *o*).

C. inflata Huds. About eighty fruits are probably referable to this species. Nine have their characteristic inflated utricles (see Fig. 1, *j*) with about twelve strong, widely spaced veins, those at the margins especially strong. The nutlets often show a very sharp kink at the base of the style.

In addition, several pieces of bark, and minute hairy bud-scales not further identifiable were present.

CONCLUSION

Outstanding features of the tree-pollen analysis are the preponderance of birch and pine pollen, the former associated with the abundant birch fruits. Presumably most of the local birch was the tree *B. verrucosa* Ehrh. although the evidence shows that the dwarf birch and the hybrid *B. nana × B. pubescens* were probably present also. The warmth-loving trees are represented by 15 % of oak pollen (variable in shape and corroded), a trace of alder,

and 3% of hazel. Willow pollen is abundant (47%) and willow wood also occurs. Grass and sedge pollen together amount to almost 150% of the total tree-pollen and, although
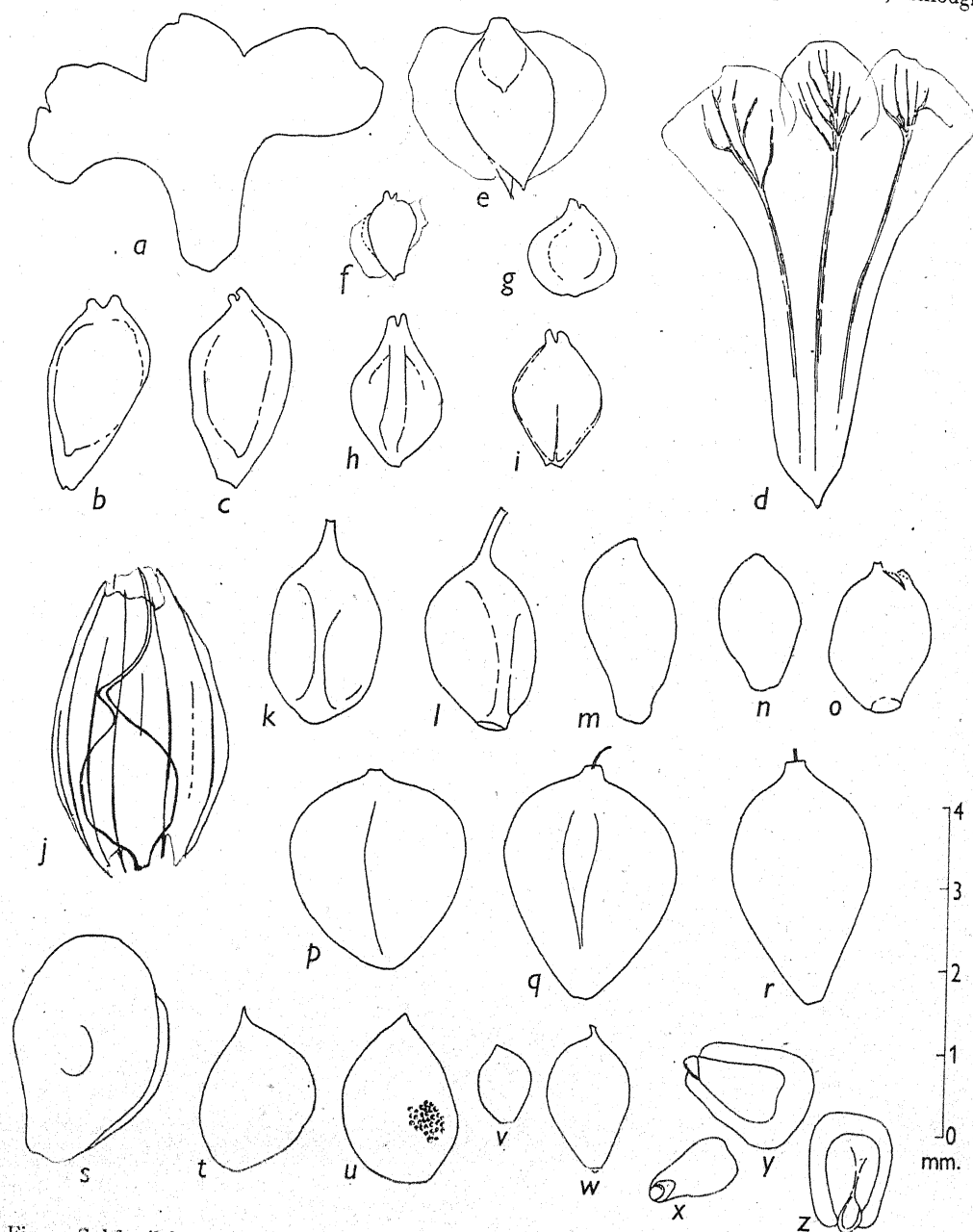
Fig. 1. Subfossil fruits from Weevil Lake, Gosport, at − 59 ft. O.D. *a*, *Betula verrucosa* Ehrh., female cone-scale; *b, c*, *B. verrucosa* Ehrh., fruits lacking wings; *d*, *B. nana × pubescens*, female cone-scale; *e*, *B.* cf. *nana × pubescens*, fruit; *f, g*, *B. nana* L., fruit; *h, i*, *B. nana* L., or *pubescens × nana*, fruit; *j*, *Carex inflata* Huds., fruit; *k, l*, *C. inflata* Huds., nutlets; *m, n*, *C. disticha* Huds., nutlets; *o*, *C. goodenowii* Gay, nutlets; *p, q, r*, *Scirpus lacustris* L., fruits; *s*, *Potamogeton*, cf. *obtusifolius*, stone; *t, u*, *Ranunculus flammula* L., achenes, *u* showing a patch of the surface pitting; *v*, *Urtica dioica* L., fruit; *w*, *Scirpus fluitans* L., fruit; *x, y, z*, *Lycopus europaeus* L., *x* without inflated border, *y* showing outer face of nutlet, *z* showing inner face.

possibly to some extent locally derived, this certainly supports the view that conditions during deposition were those of open birch-pine-willow woodland. There seems good reason to refer the sample to zone IV of our series for England and Wales (Godwin, 1940). The deposit is a shallow-water organic nekron mud, a conclusion borne out by the presence of silt and sponge spicules as well as water-plants: the sedges no doubt came from fringing fen.

The results provide us with a clear although restricted correlation between vegetational history, land- and sea-level movements, and former distribution of certain species of the British flora. It is evident that in zone IV the eustatic rise in ocean level which led to formation of the North Sea had not yet reached -59 ft. ($-17\cdot6$ m.) O.D. in the English Channel. This falls into agreement with the presence of submerged peat of zone VIb at -54 ft. ($-16\cdot4$ m.) O.D. in Swansea Bay, and in zone VIa at -114 ft. (-35 m.) O.D. off the Norfolk coast (Godwin, 1943). In view of the many problems which turn upon knowledge of when last the English Channel was dry land, it is clear that further investigation of such deeply submerged Channel peats as these would be of great interest.

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CONTRIBUTIONS TO THE ECOLOGY OF BRACKEN (*PTERIDIUM AQUILINUM*). III. FROND TYPES AND THE MAKE-UP OF THE POPULATION

By ALEX S. WATT

Botany School, Cambridge

(With 5 figures in the text)

CONTENTS

We have seen that the height of the frond varies with position on the plant and with age of the short shoot carrying it. It remains to be considered how the parts of the frond vary. Any differential changes would provide useful criteria for distinguishing fronds from different positions on the plant or fronds of different ages. The criteria can then be applied in the assessment of the make-up of a mixed population such as that in the hinterland. The presentation of the analysis is preceded by a note on some factors affecting the relative length of the lamina and the petiole.

THE GROWTH OF THE FROND AFTER EMERGENCE

The emergent frond first completes the extension of the petiole before the lamina appreciably unfolds. Data substantiating this familiar phenomenon are given in Table 1 and graphed in Fig. 1. The time difference in the period of growth of petiole and lamina is important because the conditions prevailing during the extension of each may be appreciably different. The young frond usually emerges at a time when the reserves of moisture in the soil are adequate but also when late frosts may do much damage, either by killing the frond or merely crippling it. The killed frond is eliminated but the crippled frond usually remains, its lamina damaged to varying degrees by the killing of the younger unfolding parts. In some years nearly every frond is to some extent affected and in extreme examples only the basal pinnae remain. Thus in surviving fronds a petiole of

Table 1. *Length in inches of petiole and lamina during the early growth of two fronds in May* 1943

Date	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Length of petiole	5·4	5·7	5·7	7·7	8·4	8·8	9·4	9·8	10·0	10·1	10·1	10·1	—	10·1	—
Length of lamina	1·2	1·3	1·4	1·7	2·0	2·2	2·5	3·0	4·0	4·8	5·4	6·1	—	8·5	—
Length of petiole	3·4	3·9	4·4	5·4	6·2	6·6	7·4	8·4	9·4	10·0	10·2	10·4	10·4	10·4	10·4
Length of lamina	0·8	0·9	0·9	1·1	1·3	1·3	1·5	1·7	2·4	2·9	3·3	3·8	4·6	7·0	8·0
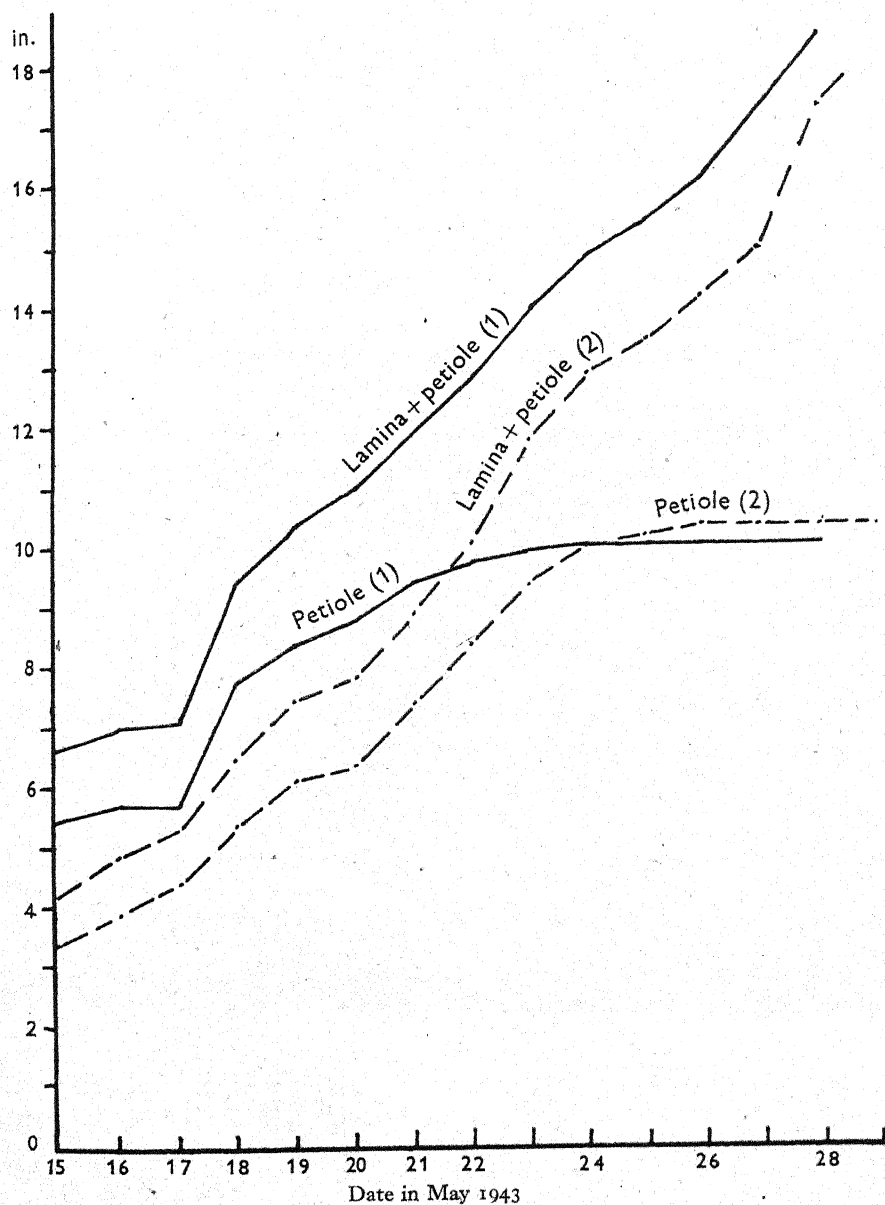
Fig. 1. Early extension growth in two fronds showing the rates of growth of petiole and lamina. The growth of the petiole is almost complete before the lamina appreciably unfolds.

normal length may carry a subnormal lamina and the ratio amina/petiole is affected. Again as the season advances the water reserves in the soil may fall sufficiently to limit the full growth of the lamina. This probably accounts for the sudden fall in the length of the pinnae near the apex observed in some years when the lamina as a whole has a mucronate apex instead of an acute one. Further, all fronds do not emerge at the same time and the laminae of those emerging late may extend under the conditions of weaker illumination below a canopy formed by those emerging earlier. These observations are made merely to indicate that while the absolute lengths of petiole and lamina may vary from year to year the relation between them may also vary. It should be added that in the marginal belt only those fronds not appreciably crippled by frost have been used in the calculations: in this way 7%, fairly uniformly distributed along the transect, were eliminated.

THE MARGINAL PLANT (AREA E, TRANSECT C, 0–80 FT.)

The general relation to position on the plant of length of lamina, total petiole, petiole and the ratios lamina/petiole and lamina/total petiole, based on the means of 10 ft. sections

The data for height and depth of origin have already been given (Watt, 1943, quoted as Pt. II). The data in Table 2 show that along the marginal plant the length of lamina, total

Table 2. *Area E, transect C, 1934. Mean length in inches of lamina, petiole, depth of origin and total petiole and the means of the ratios, lamina/petiole and lamina/total petiole*

Sections in ft. ...	Marginal plant								Hinterland		
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–115
No. of fronds	9	12	20	21	22	18	26	14	16	14	20
Mean length of lamina in in.	25·44	28·83	28·88	25·12	23·04	21·81	21·77	22·46	17·31	14·89	17·35
Mean length of petiole in in.	6·11	13·50	17·48	18·93	16·45	15·00	12·94	14·71	9·38	7·21	8·60
Mean depth of origin in in.	7·72	6·25	4·38	4·02	3·32	3·53	4·54	4·14	3·81	2·82	3·45
Mean length of total petiole in in.	13·83	19·75	21·86	22·95	19·77	18·53	17·48	18·85	13·19	10·03	12·05
Mean lamina/petiole	5·20	2·34	1·71	1·31	1·50	1·50	1·76	1·54	1·97	2·04	2·09
Mean lamina/total petiole	1·90	1·51	1·35	1·11	1·24	1·20	1·27	1·20	1·35	1·49	1·47

petiole (petiole + depth of origin) and petiole in general rise to a maximum then fall from it: there is, however, a slight rise in the last section.

The length of the petiole rises much faster than the length of the lamina, while the falls from the maxima proceed at about the same rate. The result is that the ratio lamina/petiole is high in the first section, falls rapidly to a minimum at 31–40 ft., where the petiole is longest and the lamina has already begun to fall: thereafter the ratio is slightly higher than the minimum although the lowest values in the sections from 40 to 80 ft. are not significantly different from it. A similar sequence is shown by the ratio lamina/total petiole.

Thus from the data it is clear that fronds of equal height on either side of the maximum may be distinguished by the difference in the ratio between lamina and petiole. Fronds

nearer the apex of the plant, particularly the marginal outposts, have short petioles, a lamina of moderate length and therefore a high ratio, whilst the contributions made by the long petiole to the length of fronds of similar height beyond the maximum are much greater and the ratio correspondingly smaller. It follows also that where the ratios are the same from sets of fronds on either side of the maximum, the set nearer the apex is taller.

Although no measurements have been made and no estimates formed of the percentage occurrence of fronds of different thickness of petiole along the transect, fronds up to and including the zone of maximum height have in general stout petioles: those from the posterior part of the plant are in general more slender. In each zone there is a mixture but from the anterior part of the plant fronds with stout petioles clearly preponderate, the reverse relation holding for the posterior part.

The statistical relation between position on the marginal plant and length of lamina, total petiole, petiole, lamina/petiole and lamina/total petiole

The plant in two parts: the anterior (o–30 ft.) and the posterior (31–80 ft.). Only the partial correlations need be referred to here (Table 3).

In the anterior part of the plant all the variables, except the lamina/petiole ratio change significantly with position; height, lamina, petiole, total petiole have a significant positive correlation, lamina/total petiole a significant negative one. It should, however, be noted that the total correlation for position and lamina/petiole is significant.

In the posterior part, height, lamina, petiole and total petiole fall significantly: lamina falls least, as it rises least in the anterior part. There is a very weak significant and positive correlation between lamina/petiole and position; the lamina/total petiole shows none.

As to the relation between depth of origin and position, note that there is a highly significant negative total correlation in the anterior part ($-$o·8106): there is no significant change in the posterior ($+$o·1367).

The plant in three parts: fore (o–20 ft.), mid (21–40 ft.) and hind (41–80 ft.). The maxima for the lamina and for the petiole do not coincide, the maximum for the lamina being reached earlier. This is not an accidental feature for the data from the permanent transect for each of the years 1936–41 consistently show this, although the maximum for the petiole does not always lie in the section next beyond.

Recognizing then a mid region to cover the turning-points of lamina and petiole, we find in the fore part (o–20 ft.) similar results (Table 3) to those for the anterior zone (o–30 ft.): there are positive and significant partial correlations for height, lamina, petiole and total petiole, and a significant negative value for the ratio lamina/total petiole. Once again the value for the partial correlation between position and lamina/petiole is not significant, although that for the total correlation is.

In the mid part there are no significant relations with position for the height of the frond and its parts: the ratios on the other hand show significant, though weak, partial correlations. It may be noted in passing that, though the values are not significant, that for lamina is now negative, while the value for petiole remains positive.

In the hind part, all the values are low, those for height, petiole and total petiole being just significant and negative: the lamina and the ratios show non-significant values. Thus, the divergence in values for the petiole (and total petiole) and the lamina are not reflected

Table 3. *Area E. Means, coefficients of variation and correlation from the whole marginal population (0–80 ft.), parts of it and from the hinterland. The parts of the frond as percentages of the total height are given in brackets*

Position of sample: distance in ft. from outpost fronds ...	Marginal plant						Hinterland	
	0–30	31–80	0–20	21–40	41–80	0–80	81–115	c. 300
No. of fronds	41	101	21	41	80	142	50	50
Means:								
Height in in.	41·93	38·41	37·71 (84·72)	45·17 (91·70)	36·93 (90·64)	39·43 (90·1)	25·11 (88·5)	21·13 (87·5)
Lamina in in.	28·11	22·85	27·38 (61·55)	26·95 (54·71)	22·25 (54·61)	24·37 (55·7)	16·65 (58·7)	14·25 (59·0)
Petiole in in.	13·82	15·56	10·33 (23·22)	18·22 (36·99)	14·68 (36·03)	15·06 (34·4)	8·46 (29·8)	6·88 (28·5)
Total petiole in in.	19·35	19·40	17·11 (38·45)	22·31 (45·29)	18·49 (45·39)	19·39 (44·3)	11·73 (41·3)	9·90 (41·0)
Depth in in.	5·53	3·84	6·77 (15·23)	4·09 (8·30)	3·82 (9·37)	4·33 (9·9)	3·27 (11·5)	3·02 (12·5)
Lamina/petiole	2·66	1·53	3·567	1·506	1·585	1·856	2·038	2·138
Lamina/total petiole	1·52	1·21	1·674	1·231	1·233	1·298	1·435	1·471
Coefficient of variation:								
Height	—	—	4·400	1·892	1·733	1·486	3·863	3·509
Lamina	—	—	2·932	2·949	2·446	1·834	4·065	3·983
Petiole	—	—	11·07	2·386	2·267	2·321	4·340	3·853
Total petiole	—	—	5·631	2·047	1·770	1·597	3·753	3·727
Depth	—	—	4·843	4·407	3·743	3·166	3·971	5·654
Lamina/petiole	—	—	17·96	4·916	3·509	6·293	3·559	4·333
Lamina/total petiole	—	—	4·768	3·754	3·023	2·336	2·982	3·956
Correlation coefficients:								
P=0·05 level of significance	0·3084	0·1956	0·4329	0·3085	0·2202	0·1678	0·2788	0·2788
Position and height	+0·7718	−0·4429	+0·8650	−0·0988	−0·2006	—	−0·0929	—
Position and lamina	+0·3401	−0·1973	+0·4994	−0·2380	−0·0465	—	−0·0462	—
Position and petiole	+0·8493	−0·5556	+0·9058	+0·3091	−0·3588	—	−0·1423	—
Position and total petiole	+0·7449	−0·4761	+0·8311	+0·1940	−0·2641	—	−0·1571	—
Position and depth	−0·8106	+0·1367	−0·7319	−0·2605	+0·3069	—	−0·1623	—
Position and lamina/petiole	−0·6080	+0·2236	−0·6285	−0·3406	+0·1002	—	+0·0478	—
Position and lamina/total petiole	−0·5853	+0·1057	−0·6773	−0·4024	−0·0034	—	+0·1249	—
Depth and height	−0·6297	+0·0872	−0·4624	+0·0445	+0·0411	−0·0711	+0·4747	+0·4674
Depth and lamina	−0·0771	+0·2577	−0·0353	+0·1073	+0·2220	+0·2828	+0·5016	+0·5426
Depth and petiole	−0·4745	−0·1112	−0·6482	−0·1150	−0·2219	−0·4703	+0·3371	+0·3943
Depth and total petiole	−0·5319	−0·1849	−0·4283	+0·2881	+0·1238	−0·0605	+0·6193	+0·6251
Depth and lamina/petiole	+0·6107	+0·2543	+0·5928	+0·1510	+0·2283	+0·5405	+0·2223	+0·1825
Depth and lamina/total petiole	+0·4680	+0·0029	+0·4759	−0·0707	+0·0147	+0·3353	−0·0906	−0·1707
Partial correlation coefficients:								
P=0·05 level of significance	0·3124	0·1962	0·4438	0·3124	0·2215	0·1684	0·2819	—
Position and height	+0·5743	−0·4601	+0·8717	+0·0177	−0·2242	—	−0·0183	—
Position and lamina	+0·4778	−0·2429	+0·6955	−0·2189	−0·1236	—	+0·0412	—
Position and petiole	+0·8809	−0·5489	+0·8315	+0·2910	−0·3132	—	−0·0943	—
Position and total petiole	+0·6326	−0·5148	+0·8408	+0·2912	−0·3198	—	−0·0731	—
Position and lamina/petiole	−0·2437	+0·1971	−0·3548	−0·3157	+0·0325	—	+0·0872	—
Position and lamina/total petiole	−0·3981	+0·1063	−0·5490	−0·4369	+0·0012	—	+0·1398	—
Depth and height	+0·0293	+0·1766	+0·4988	+0·0731	+0·1102	—	+0·4677	—
Depth and lamina	+0·3603	+0·2847	+0·5594	+0·0483	+0·2485	—	+0·5012	—
Depth and petiole	+0·6920	−0·0427	+0·0506	−0·2130	−0·1258	—	+0·3214	—
Depth and total petiole	+0·1843	+0·3151	+0·4750	+0·3575	+0·2234	—	+0·6094	—
Depth and lamina/petiole	+0·2537	+0·2317	+0·2508	+0·0686	+0·2087	—	+0·2334	—
Depth and lamina/total petiole	−0·0134	−0·0118	−0·0395	−0·1985	+0·0165	—	−0·0718	—

in the correlation values of the ratios with position. The partial regression lines for lamina and total petiole are drawn in Fig. 2.

The depth of origin shows in the fore part a high negative significant total correlation with position (−0·7319): in the mid part a non-significant negative value (−0·2605) and in the hind part a positive and significant one (+0·3069).

This division of the marginal plant into three parts thus obscures certain relations as it brings out others. It obscures the full extent of the fall in height of frond and its parts on
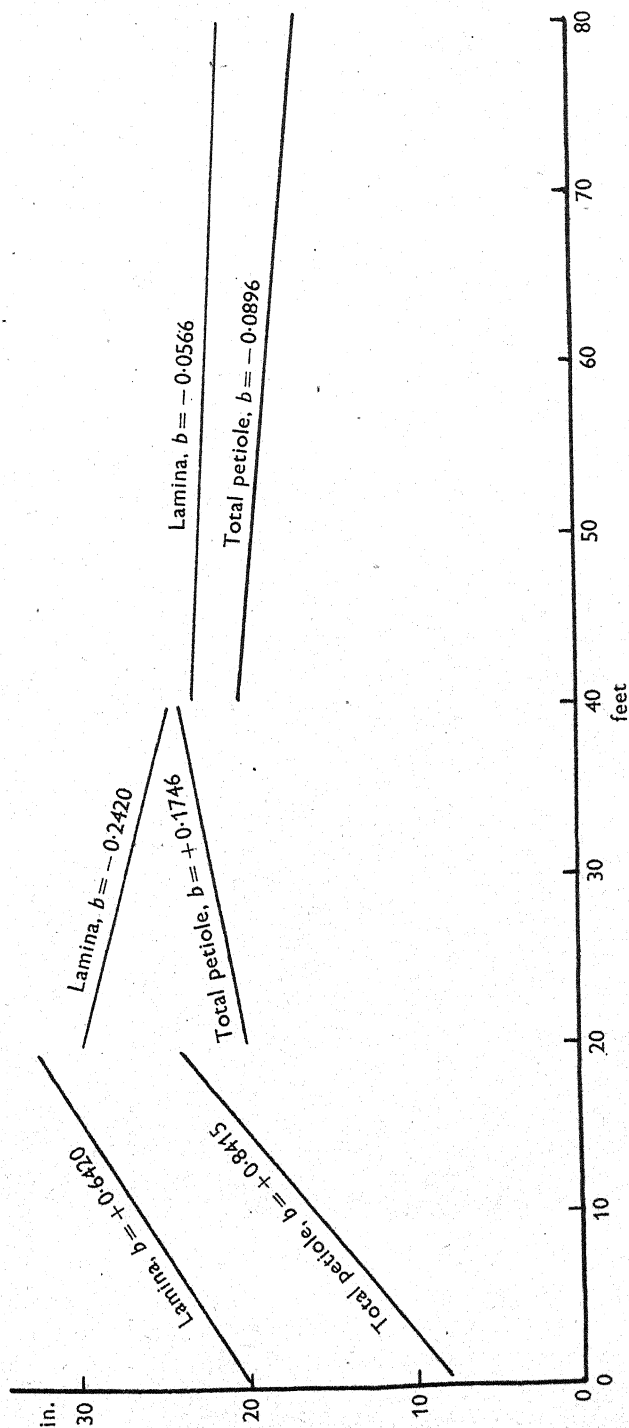
Fig. 2. The partial regression lines for lamina and total petiole on position in the fore, mid and hind zones of the marginal plant.

the posterior part of the plant, for the major drop coincides with the division between the mid and hind zone. On the other hand it brings out the significant change in depth, for the minimum coincides with the first section in the hind part.

The increase in depth in the hind part is due to the progressive replacement of old shoots by younger ones, that is, there is a change in the make-up of the population in whose mean depth of origin the increasing age of the short shoots is more than offset by their fall in number through dying back and by the entry of new ones of deeper origin. There is in fact a definite change in the representation of the different depth (or age) classes.

The statistical relation between number of nodes and length of lamina,
petiole, total petiole, lamina/petiole and lamina/total petiole

In Table 4, the means from selected places across the marginal belt at Red Lodge bear out the sequence of change in the frond parts and the ratios lamina/petiole and lamina/total petiole already noted for the transect in area E.

Table 4. *Red Lodge*, 1942. *Means, coefficients of variation and correlation from samples at selected places along the marginal plant and in the hinterland*

	Marginal plant			Hinterland	
Position of sample: distance in ft. from outpost fronds ...	0–7	21–23	31–35	41–45	75–79
No. of fronds	30	50	50	50	50
Means:					
Height in in.	19·16	48·01	36·42	31·15	23·89
Lamina in in.	17·41	32·21	25·90	22·60	16·80
Petiole in in.	1·75	15·80	10·53	8·55	7·09
Total petiole in in.	8·14	19·88	15·21	13·46	10·60
Depth in in.	6·39	4·08	4·68	4·905	3·510
No. of nodes	3·94	9·04	9·98	8·20	12·14
Lamina/petiole	13·38	2·127	2·608	2·924	2·699
Lamina/total petiole	2·235	1·670	1·778	1·721	1·647
Coefficients of variation:					
Height	2·540	1·643	2·510	2·997	3·348
Lamina	2·766	2·087	2·817	3·423	3·814
Petiole	9·186	2·862	3·546	4·538	4·730
Total petiole	3·823	2·473	3·173	3·313	3·625
Depth	4·226	3·861	3·850	4·878	5·227
Correlation coefficients:					
$P = 0.05$ level of significance	0·3556	0·2788	0·2788	0·2788	0·2788
No. of nodes and height	−0·3435	−0·4742	−0·4240	−0·5225	−0·5830
No. of nodes and lamina	−0·3051	−0·2142	−0·3137	−0·5285	−0·5585
No. of nodes and petiole	−0·0996	−0·5081	−0·4240	−0·1328	−0·2844
No. of nodes and total petiole	−0·6255	−0·6526	−0·5261	−0·5013	−0·5255
No. of nodes and lamina/petiole	−0·3875	+0·3016	+0·1466	−0·2125	−0·1594
No. of nodes and lamina/total petiole	+0·2770	+0·2507	+0·2153	−0·0863	−0·0503

We have seen (Pt. II) that, at a given position on the plant, the height of the frond falls with age, but since the contributions of petiole and lamina to height vary it does not follow that each is similarly related to age. In fact for the lamina at maximum height and at 31–35 ft. there is a significant fall only at the latter position—and the association is weak— while within the range of age represented at maximum height there is no corresponding fall. Comparison of the grouped data in Table 5 shows that it is the older fronds which respond, the younger varying little with age. Incidentally these grouped data should be

compared with the corresponding data for the two hinterland samples where an immediate response to age is manifest. The difference between the contrasted sets may be related to the difference in vigour (size) of the plants.

The petiole and total petiole on the other hand show a fall with age at maximum height and at 31–35 ft., and for total petiole the fall is faster at the former position (Fig. 3).

Table 5. *Red Lodge, 1942. Number of fronds, mean length of lamina, petiole, total petiole, the ratios lamina/petiole and lamina/total petiole for node categories in samples at selected places along the marginal plant and in the hinterland*

Position of sample: distance in ft. from outpost fronds	Node category	No. of fronds	Mean length of lamina	Mean length of petiole	Mean length of total petiole	Mean ratio lamina/ petiole	Mean ratio lamina/ total petiole
			Marginal plant				
0–7	1–5	21	17·93	1·86	8·74	11·78	2·16
	6–10	9	16·58	1·47	7·00	12·05	2·38
	11–15	1	15·00	2·00	5·75	7·50	2·61
21–23	1–5	12	32·37	17·96	23·25	1·86	1·41
(region of	6–10	20	33·36	16·03	19·93	2·19	1·72
max. height)	11–15	15	31·67	14·90	18·43	2·15	1·73
	16–20	3	26·83	10·17	13·34	2·69	2·05
31–35	1–5	15	26·65	11·58	17·33	2·36	1·58
	6–10	15	27·47	10·80	15·30	2·77	1·87
	11–15	12	25·13	10·04	14·35	2·67	1·82
	16–20	5	23·85	9·75	13·35	2·50	1·84
	21–25	0	—				
	26–30	1	23·50	7·50	12·50	3·13	1·88
	31–35	2	19·38	6·88	9·63	2·91	2·03
			Hinterland				
41–45	1–5	23	25·92	9·79	15·86	2·98	1·69
	6–10	14	19·66	7·30	11·52	2·98	1·77
	11–15	7	22·57	7·29	11·15	3·34	2·05
	16–20	2	14·50	7·00	9·63	1·97	1·42
	21–25	2	18·00	10·25	14·13	1·71	1·26
	26–30	2	17·75	7·25	10·75	2·56	1·66
75–79	1–5	17	20·41	7·68	12·27	3·22	1·74
	6–10	8	16·91	7·78	10·97	2·20	1·55
	11–15	8	14·22	7·03	10·03	2·17	1·45
	16–20	10	15·25	6·40	9·40	2·92	1·77
	21–25	0	—	—	—	—	
	26–30	3	14·50	6·00	9·33	2·60	1·59
	31–35	3	12·33	6·17	8·17	2·02	1·54
	36–40	1	11·00	5·00	7·00	2·20	1·57

This lack of responsiveness of the lamina from younger shoots at maximum height appears to account for the significant rise in the lamina/petiole ratio with age. But the value is low and there is no significant correlation between age and lamina/total petiole. At 31–35 ft. neither ratio shows a significant relation to age. Reference to the grouped data (Table 5) shows considerable variation in the ratios with the lowest values for the youngest node category. The explanation of this irregularity is not obvious: it is perhaps related to the different times of emergence and the conditions (e.g. illumination) surrounding the frond during its extension.

For the reasons given in Pt. II little reliance can be placed on the data from the 0–7 ft. sample. The gap in our analysis may however be filled by using the alternative correlate to number of nodes, namely, depth of origin, in samples where position has been noted and its effect eliminated by calculating the partial correlation. The partial correlations

(Table 3) between depth and the variables, height, length of lamina and total petiole for the o–20 ft. zone in the transect show positive and significant values: that is, at this given position there is a rise with depth (or a fall with age). The non-significant values for the ratios show no change with depth (or age). Thus only the non-significant correlation between petiole and depth fails to conform to the general pattern.
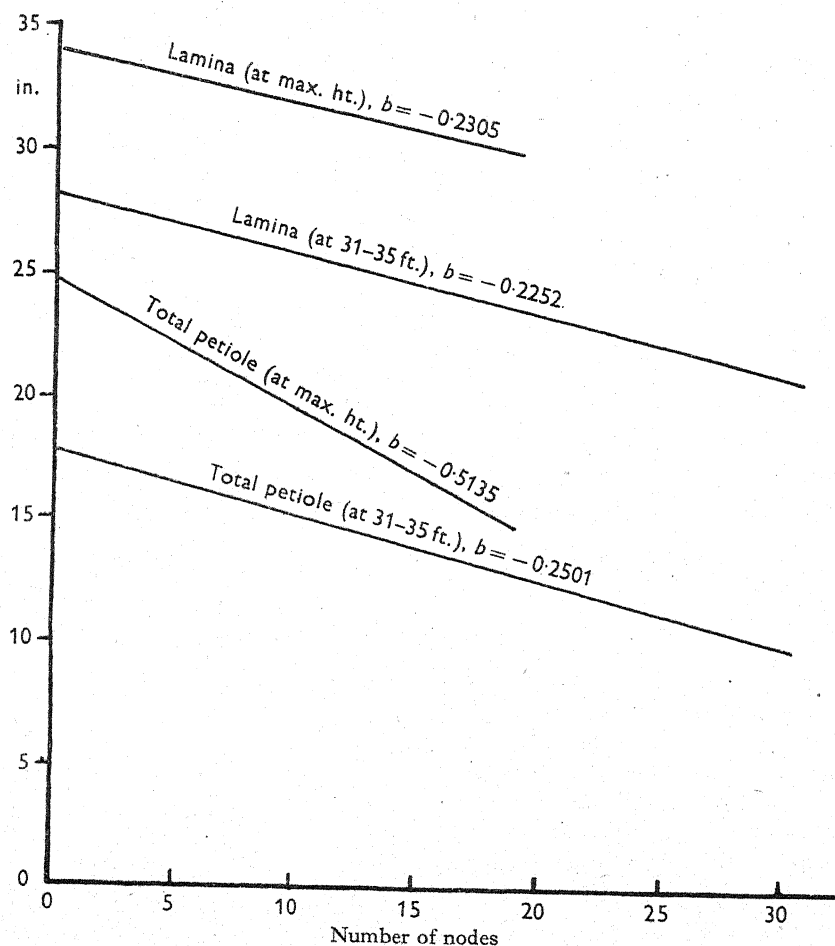
Fig. 3. The regression lines for lamina and total petiole on number of nodes at maximum height and at 31–35 ft. at Red Lodge.

When, however, the test is extended to the o–30 ft. zone (Table 3) only the lamina and the ratios show values consistent with those for o–20 ft.: the petiole now shows a high correlation and height none at all.

Similar inconsistencies are shown in the posterior half of the plant (31–80 ft.) and in the mid and hind regions. Thus in the posterior half, height, petiole and lamina/total petiole show no significant correlation with depth, while lamina, total petiole and lamina/petiole show significant though weak association. In the mid region only total petiole shows a significant correlation with depth, and in the hind region total petiole and lamina. When, however, the values for the posterior part and the mid and hind regions are com-

pared the data are consistent among themselves in showing no correlation between depth and height, petiole, lamina/total petiole and a significant positive correlation with total petiole. Only the lamina and lamina/petiole give varying results, but in no case is the correlation high.

These results differ from those obtained at 31–35 ft. at Red Lodge and the validity of the substitution of depth for number of nodes may well be questioned. To test the point the correlations between the variables and depth for this sample have been worked out: the results for height, lamina, petiole, total petiole, lamina/petiole and lamina/total petiole are respectively $+0.4783$, $+0.3493$, $+0.4883$, $+0.7495$, -0.2160 and -0.3927, that is, for all but lamina/total petiole there is fairly good agreement.

Further, a sample of 50 fronds at 40–50 ft. in the transect gives with depth for the same variables in the order given above $+0.3635$, $+0.2980$, $+0.1892$, $+0.4590$, $+0.0224$ and -0.0748; that is, for all but lamina there is agreement in significance with the values for the relation between the variables and number of nodes at Red Lodge.

There appears therefore to be some difference between the population from a circumscribed position on the plant and one covering the distal part. The possibility that density is such a difference is excluded as in the hind part the relation between depth and height and depth and the ratios (eliminating position and density) has been worked out: the values are found to be virtually the same, as for those with density ignored.

Taken as a whole, then, depth of origin is a satisfactory substitute for number of nodes in samples taken from a circumscribed position on the plant. Whether it is so or not in samples covering the distal portion of the plant cannot be directly tested for lack of the necessary data, but it is relevant to point out that the depth of origin of the frond and its use as a substitute for age will depend in part on the depth of the rhizome bearing the shoots and that this changes with a change in structure of the rhizome synusia has already been indicated (Pt. II). Changes in structure covering the whole of the distal portion of the plant may well upset a high correlation shown by a narrowly circumscribed part. And the lower values for the 10 ft. section (41–50 ft.) of the transect compared with those from an axial distance of 4 ft. (31–35 ft.) at Red Lodge may indicate the rapidity of the change and the limits on the plant within which high correlations may be expected.

If then we omit the anomalous region of maximum height which covers the turning-points in the values of lamina and petiole, or absorb its two halves in a division of the plant into an anterior and a posterior part, we can say that by and large there is a change with position not only in the height of the frond but also in its parts and that at any narrowly circumscribed position there is a fall with age.

An important point emerging from the analysis is that the ratio lamina/total petiole remains more or less constant with age, but varies with position: the unequal rates of change in length of lamina and total petiole in the anterior part give a falling ratio with position, in the posterior part the similar rates of fall give no significant correlation with position.

The ratio lamina/petiole also does not vary with age and shows in the posterior part (41–80 ft.) only a weak significant increase with position. In samples, however, where position cannot be evaluated and the total correlation with depth only is in question, significant values are obtained both in the fore and hind position of the plant: of these two values the former is the greater.

Since fronds near the apex of the plant generally lie deeper the question arises whether

the total petiole of fronds near the apex is inherently relatively shorter or whether it is in some way affected by the medium through which it grows. It may be that in places where the whole rhizome is shallow this does not hold, but there are no data on this point.

Characterization of frond types

Fronds from near the apex of the plant (pioneers) are stout, deep-set, short-petioled with moderate length of lamina and high ratios both for lamina/petiole and lamina/total petiole. At maximum height the fronds are still stout, tall, fairly shallow set with long lamina and long petiole and low values for the ratios. Fronds from the posterior part of the plant are less robust, fairly shallow (often very shallow) of medium height with relatively low values for the ratios but not so low as for the region of maximum height. Sets of fronds of equal height from the anterior and posterior parts respectively are distinguished not only by their robustness, but also by the higher ratios for the anterior part.

THE HINTERLAND PLANT

Two sets each of two samples, one from area E and one from Red Lodge are available for the study of the hinterland population. In each set one sample comes from just behind the marginal plant, the other more remote in the hinterland. Comparison can thus be made between the hinterland samples among themselves and with the whole marginal plant (from area E only, as there are no data for the whole marginal plant from Red Lodge) and a study made of the change from the marginal plant to the remote hinterland.

The change from the marginal plant to the remote hinterland

The transect from 80 to 115 ft. covers the part of the hinterland next to the marginal plant, and in it the relation of the variables to position has been worked out. The data in Table 3 show no significant relation between position and any variable: in this the population differs from any of the parts into which the marginal plant has been divided. Also a comparison of the total correlations between depth and the variables for the whole marginal plant (Table 3) and for the hinterland part of the transect show differences in sign and/or of magnitude which confirm the conclusion reached in Pt. II that the make-up of the population in the near hinterland (and the remote hinterland, as we shall see presently) is, taken as a whole, radically different from that of the marginal plant.

The fall in the height of the frond from the margin into the hinterland has already been related to the fall in the size of the plant (Pt. II). The data (Table 3) show a similar fall in the length of lamina, total petiole and petiole, the differences between successive pairs of means being significant in all, as they are also for height. There is also a fall in the depth of origin, but whereas there is a significant fall from the marginal plant to the near hinterland, there is no significant difference between the depths of the two hinterland samples.

Contrasted with these progressively falling values the means of both ratios show a rise, but those for lamina/petiole are not significantly different. The lamina/total petiole from the marginal population is, however, significantly less than either of the other two which do not differ significantly from each other.

Thus the fall in size of the plant is reflected in the dimensions of the frond.

The near and remote hinterland samples

The conclusion that the smaller dimensions of the frond are due to the smaller size of the plant is, however, valid only where similar populations are being compared. The

similarity in depth and in the ratio lamina/petiole suggests a close relation between the two hinterland samples and the question arises how far, irrespective of the absolute dimensions of the frond, the hinterland populations agree with each other. The application of various tests shows that the populations are essentially identical.

The means of the parts of the frond have been expressed as a percentage of the mean total height (Table 3). The similarity of the values in the mean frond type suggests identity in the make-up of the two hinterland populations. And this is confirmed by the closely similar values for the correlation coefficients between depth and the variables and for the coefficients of variation (Table 3).

Again, a comparison of the coefficients of variation and of correlation of the two hinterland samples from Red Lodge (Table 4) shows good agreement both among themselves and with those from area E. The minor differences between the two areas may be related to the different years in which the data were obtained and in particular to spring frost which in 1934 (area E) was serious and negligible in 1942 (Red Lodge).

Since the make-up of the populations of the near and remote samples is similar the difference in the absolute dimensions of the frond may be validly related to the difference in size of the plant.

Comparison between the marginal and hinterland populations

Applying the same criteria as used in comparing the near and remote samples of the hinterland in a comparison of the marginal with the hinterland plant we find numerous striking differences: the mean frond type differs in its proportions, the correlation coefficients of the variables with depth are all different either in sign or in magnitude and the same holds for the coefficients of variation which are all (except for lamina/petiole) less for the marginal plant than for the hinterland.

Thus the constitution of the hinterland population is different from that of the margin: hence differences in absolute dimensions may be due to this rather than to a fall in size of the plant. In fact, both plant size and population make-up seem to contribute.

This can be seen from the data in Table 6 which throws light upon the make-up of the population and compares frond dimensions from corresponding depth classes in the marginal and the two hinterland populations.

The data show that in corresponding depth classes there is a fall in frond dimensions in the three contrasted samples. Thus the conclusion is justified that a fall in frond dimensions runs parallel with a fall in size of the plant.

But the data also show an essential difference between the marginal and the hinterland population, in the distribution of fronds in depth classes (Table 9). In all three samples the mode lies in the 3–4 in. depth class, but the range of depth classes represented and their distribution about the mode are different, being narrower in range and more symmetrically distributed in the two hinterland samples, but in the marginal covering a wide range with a preponderance of fronds in depth classes greater than the modal. Thus compared with the marginal the hinterland population is 'older' (i.e. there are relatively more shallow set fronds from older shoots). This is reflected in the lower mean depth (3·27 and 3·07 in. in the hinterland samples and 4·33 in. in the marginal) and confirmed by the greater mean number of nodes (12·14) in the remote hinterland at Red Lodge than in the oldest part of the marginal plant (9·98). It should, however, be pointed out that the difference between the distribution of fronds in depth classes in the marginal and hinterland samples

(area E, 1934) is accentuated by the differential action of spring frosts against the deeper-lying fronds of the pioneer type which tend to emerge earlier.

Besides the difference in size of the fronds there are then two important differences between the marginal and the hinterland populations, namely, age and the arrangement of the fronds.

The hinterland population as a whole is remarkably uniform in the total correlations of the frond variables with depth: height, lamina, petiole, total petiole all show positive and significant values with depth, that is, there is a fall with age. The values in the marginal plant are by contrast irregular, lamina showing a low positive value, petiole a negative one and height and total petiole no significant relation with depth. Now the values with depth from the hinterland populations closely parallel those from the circumscribed population at 31–35 ft. from Red Lodge suggesting a similarity in their make-up, in fact a population in which the frond type is relatively uniform, whose differences are primarily related to

Table 6. *Mean length (in inches) of the frond and its parts and the mean ratios lamina/petiole and lamina/total petiole per depth category in the population of the margin, the near (81–115 ft.) and remote (at 300 ft.) hinterland respectively*

Depth class ...		0–0·9	1–1·9	2–2·9	3–3·9	4–4·9	5–5·9	6–6·9	7–7·9	8–8·9	9–9·9	10–10·9
Height:	0–80 ft.	—	40·50	38·61	39·52	40·97	39·90	39·23	36·87	35·66	33·00	33·00
	81–115 ft.	—	14·66	22·47	25·92	29·19	29·70	—	—	—	—	—
	at 300 ft.	14·00	17·90	18·90	22·90	25·10	23·00	—	—	—	—	—
Lamina:	0–80 ft.	—	23·75	22·79	22·81	25·31	25·69	24·65	26·56	28·50	31·00	27·00
	81–115 ft.	—	8·83	15·04	17·00	19·25	20·70	—	—	—	—	—
	at 300 ft.	7·70	12·50	12·40	15·80	16·60	17·70	—	—	—	—	—
Petiole:	0–80 ft.	—	16·75	15·82	16·71	15·66	14·21	14·58	10·31	7·16	2·00	6·00
	81–115 ft.	—	5·83	7·43	8·92	9·94	9·00	—	—	—	—	—
	at 300 ft.	6·30	5·40	6·50	7·10	8·50	5·30	—	—	—	—	—
Total petiole:	0–80 ft.	—	18·38	18·26	20·04	19·95	19·47	20·85	17·53	15·24	11·50	16·00
	81–115 ft.	—	7·25	9·85	12·21	14·22	14·30	—	—	—	—	—
	at 300 ft.	7·05	6·84	8·90	10·55	12·95	10·43	—	—	—	—	—
Lamina/petiole:	0–80 ft.	—	1·41	1·49	1·43	1·65	1·97	1·86	2·84	4·19	15·50	4·50
	81–115 ft.	—	1·49	2·05	2·05	1·99	2·38	—	—	—	—	—
	at 300 ft.	1·27	2·36	1·92	2·22	2·04	3·38	—	—	—	—	—
Lamina/total petiole:												
	0–80 ft.	—	1·29	1·28	1·18	1·28	1·35	1·23	1·56	1·88	2·69	1·69
	81–115 ft.	—	1·20	1·53	1·43	1·35	1·43	—	—	—	—	—
	at 300 ft.	1·13	1·86	1·36	1·48	1·30	1·70	—	—	—	—	—

age and not to position. Thus, although the coefficients of variation are higher in the hinterland than in the marginal population, the wider range shown is within a given frond type.

There is also a contrast between the marginal and hinterland populations in the means of the ratios and in the total correlations with depth. As for the means the lamina/petiole of the marginal plant is not significantly less because of the high values of the deep-set pioneers, but it may be recalled that from the minimum values of both ratios at the region of maximum height there is a rise towards the end of the plant. This rise is continued into the hinterland and the data in Table 6 show that depth for depth the values are greater than in the marginal plant, that is, with a fall in size of the frond the petiole and total petiole fall faster than the lamina. A similar difference is seen at Red Lodge in the contrast between the region of maximum height and at 31–35 ft., where in corresponding node categories the values for the ratios are in general higher at the end of the plant (Table 5). There is, however, no regular rise with position.

Again, for the whole marginal plant, there are positive and significant values for the total correlations between depth and the ratios reflecting the overriding effect of the anterior part of the plant population. For the hinterland the values are not significant and this again suggests not only uniformity but a resemblance to the posterior part of the marginal population.

We may then conclude that besides differences in dimensions of the frond there are important differences between the marginal and hinterland populations in age and in the arrangement of the fronds: the hinterland population also consists of fronds more uniform in type but showing a fairly wide range in dimensions within that type, and taken as a whole a closer resemblance to the posterior part of the marginal population.

It may be added that although spring frosts in 1934 have accentuated the aged character of the population in the hinterland by reducing or eliminating pioneers, the population retains those essential features of age even in years when spring frosts are negligible or absent (cf. the data for Red Lodge, 1942, Table 4).

THE CYCLE OF PHASES IN THE HINTERLAND

The fact that the whole populations of the margin and of the hinterland are different does not exclude the possibility that component partial populations may resemble each other. The notes on the structure of the bracken community show that we may compare the sequence of zones in the marginal population with a series of even-aged forest planta-tions of increasing age: beyond the region of maximum height are the beginnings of the change to an uneven-aged community which is completed in the hinterland where the uneven-aged composition is comparable with an uneven-aged natural forest with a predominance of the older age classes. But the analogy may be extended further to the way in which the age-classes are grouped, for in the hinterland population there is not only patchiness of the fronds but these fronds tend to be grouped in age-classes, that is, fronds of a given type tend to be aggregated. Data substantiating this will be given in the next part.

Observations made on bracken, and on other plant communities both in Breckland and elsewhere had led to the formulation of the hypothesis that the plant community shows not only a static pattern but also a dynamic one, that, in fact, in the patchy bracken of the hinterland we have a pattern in space the component parts of which form a sequence in time. Now the marginal belt shows a series of zones which are both a sequence in space and in time and a comparison between components of the hinterland pattern and zones in the marginal should afford evidence of the validity of the hypothesis in a comparison of the relative dimensions of the frond and its parts.

Five phases (or aspects of the pattern) in the patchy bracken were chosen, the recogni-tion of which was based on the presence or absence of fronds and where fronds were present on the collective evidence provided by the dimensions of the visible parts of the frond, its vigour, number per unit area, the amount of litter and its state of decomposition, and associated species: that is, they were recognized partly on features provided by the frond itself and partly on features not primarily determined by frond type, although linked with it. These five stages were called for convenience, grass-heath (without fronds), pioneer, building, mature and degenerate, respectively. Only the evidence provided by the frond is considered here so that no further reference is made to the grass-heath phase.

In each of the four remaining phases sample areas, each of one square foot, were taken

and additional patches of undefined area but approximately of a square foot were chosen to augment the number of fronds.[1]

The fall in the height of the frond beyond the region of maximum height is related to the position of the frond on the marginal plant and beyond its limits mainly to the decreasing size of the plant. In the hinterland the same fall in height on the individual plant is observed but at present too little is known about variation in the size of the plant in the apparently stable community to relate differences in height to differences in size. For the moment this is ignored and the assumption made that the plants dealt with are of relatively uniform size.

In the comparison between the four phases and successive zones in the marginal population, attention may first be called to the robustness of the frond. As already mentioned no data are available from the marginal population, but fronds in the anterior half are more robust than those in the posterior. In the four phases fronds were described as robust or slender with an intermediate category accommodating those which could clearly be assigned to neither. The distribution of these in the four phases (Table 7)

Table 7. *The percentage distribution in the four phases of frond 'vigour', of June and August frosted fronds and insect-attacked fronds: also the mean height of non-frosted fronds*

Phase	Pioneer	Building	Mature	Degenerate
Robust	90·5	48·9	10	33·3
Intermediate	4·75	28·9	20	19·4
Slender	4·75	22·2	70	47·2
June frosted	0·0	0·0	12·8	6·5
August frosted	77·3	24·5	20·5	28·3
Intact	22·7	75·5	66·7	65·2
Height of intact fronds in in.	15·20	18·91	21·38	17·08
Attacked by insects	63·6	16·3	12·8	21·7

shows the changing proportion with a maximum of robust in the pioneer, falling to a minimum in the mature with a subsequent rise in the degenerate. Robust fronds preponderate in the pioneer and building phases, slender in the mature and degenerate. Thus, in a general way, pioneer and building correspond with the anterior half of the marginal plant, mature and degenerate with the posterior.

The mean values for the frond variables are given in Table 8. Successive pairs of means are significantly different in all, except for lamina in building and mature and for total petiole and number of nodes in pioneer and building. In the pioneer phase the fronds are robust, deep set, short-petioled with moderate lamina and a high lamina/petiole ratio, a description which fits the outpost fronds in the marginal belt. The moderate depth combined with a high ratio in taller, mainly robust fronds with longer lamina suggests equating the building phase with some part of the anterior zone lying between the apex and the region of maximum height: and the tall mainly slender fronds of shallow origin and a relatively low lamina/petiole ratio (and lower lamina/total petiole than in the building phase) identifies the mature phase with some part of the posterior zone. The degenerate phase presents unusual features, a combination of fronds of moderate height (about half are slender and a third robust) with moderate depth and moderate

petiole and lamina giving values which in the main are intermediate between those for mature and pioneer. This combination suggests a mixture of fronds, representative of these two phases but not between them in position because moderate stature is joined with a lamina/petiole ratio less than that found in the building phase.

In the sequence of change in the values for the dimensions of the frond and its parts it is not difficult to see a general resemblance to the change across the marginal belt: there is a rise to a maximum then a fall from it in height, lamina, petiole and total petiole and a

Table 8. *Means, coefficients of variation and of correlation in four phases of the cyclic pattern in the hinterland of area E. The parts of the frond expressed as percentages of the total height are given in brackets*

Phase	Pioneer	Building	Mature	Degenerate
No. of fronds	22	49	37	44
Means:				
Height of frond in in.	12·55	18·24	20·20	15·48
	(68·68)	(80·20)	(87·39)	(78·49)
Lamina in in.	11·15	14·77	14·19	11·69
	(59·63)	(64·96)	(61·35)	(59·29)
Petiole	1·40	3·46	6·01	3·79
	(9·05)	(15·24)	(26·04)	(19·20)
Total petiole	7·55	7·96	8·93	8·03
	(40·37)	(35·04)	(38·65)	(40·71)
Depth in in.	6·15	4·50	2·92	4·24
	(31·32)	(19·80)	(12·61)	(21·51)
Lamina/petiole	8·344	4·917	2·580	3·739
Lamina/total petiole	1·505	1·925	1·637	1·497
Nodes	7·24	9·80	15·97	11·95
Coefficient of variation:				
Height	7·867	3·060	3·820	5·344
Lamina	8·176	3·141	4·485	5·690
Petiole	14·82	5·958	4·341	7·878
Total petiole	5·245	3·638	3·626	3·278
Depth	5·719	4·142	5·484	6·955
Lamina/petiole	10·67	6·114	6·249	8·950
Lamina/total petiole	7·621	3·467	4·697	6·527
Nodes	12·89	10·23	8·294	11·08
Correlation coefficients:				
P=0·05 level of significance	0·4227	0·2817	0·3246	0·2976
Depth of origin and height	+0·2704	+0·4082	+0·1387	−0·4909
Depth of origin and lamina	+0·2895	+0·4579	+0·2464	−0·3394
Depth of origin and petiole	−0·0660	+0·0810	−0·1610	−0·6030
Depth of origin and total petiole	+0·8530	+0·7025	+0·3411	+0·4283
Depth of origin and lamina/petiole	+0·2456	+0·1522	+0·2847	+0·3652
Depth of origin and lamina/total petiole	−0·2247	−0·3658	−0·0659	−0·4588

further resemblance in the attainment of the absolute maximum for lamina in the building phase before that for petiole in the mature. Depth and lamina/petiole on the other hand fall to a minimum then rise just as in the transect. Further the maxima of the former (apart from lamina) coincide with the minima of the latter.

Since the four phases are arbitrarily selected from what may be assumed to be a continuously varying population it does not follow that the cardinal points of maxima and minima can be equated with the corresponding points in the marginal population, nor in view of the remarks made concerning the growth of the frond (p. 158) can reliance be placed on the absolute values of the ratios especially in the pioneer and degenerate phases

where, as the result of immaturity and frost damage to some fronds, the length of the lamina will be less than normal and the values of the ratios lowered: only the relations between values can be considered.

There are important differences however. The absolute values of the total petiole show little change in all four phases and the values for lamina/total petiole, while conforming to the expected in the fall from building to mature, are less than expected in the pioneer and degenerate. There is also a steeper rise in the absolute values for height, lamina and petiole in the hinterland than in the margin. In depth of origin too the values are less in the pioneer and greater in the degenerate than in corresponding parts of the margin.

Further, a restriction on the use of the data arises from the impossibility of making a direct comparison between the percentage distribution of parts of the frond in terms of the whole in the phases and in the margin because in the falling size of the frond there is no corresponding fall in depth: in the short fronds of the hinterland a higher proportion of the frond is below ground and the values for some parts above ground will be correspondingly reduced. We may therefore fall back on depth and the percentage values for lamina and total petiole which in the calculations are unaffected by depth. But even here comparison shows, especially in the building and mature phases, that the lamina is relatively longer and the total petiole relatively shorter than in corresponding parts of the margin.

Some of these differences can be explained by reference to the effect of frost on the fronds and on the make-up of the population. To carry explanation along with the phenomena, the relevant facts are given here, although the effect of frost on bracken is the subject of a subsequent part in this series. The data were obtained in August 1940, a year marked by severe frost during the previous winter, light spring frosts and exceptionally early autumn frosts. The severe winter frost by killing fronds developing earlier and reaching nearer the soil surface, chiefly affected the pioneer and building phases: and also because these fronds are least protected by a covering of bracken litter. Hence no fronds emerged in time to be affected by June frosts. The substitute pioneer and adventitious fronds emerging late failed to reach maturity (some were only a few inches high) before the onset of autumn frosts: consequently a high percentage was crippled, and much higher (and more seriously) in the pioneer than the building phase (Table 7).

On the other hand the fronds in mature and degenerate, being older, develop later and their better protection from winter frost means that a percentage emerge early enough to be crippled by light spring frosts. As in pioneer and building the substitute fronds fail to reach maturity before being crippled by the August frost—and a higher percentage (and more seriously) in the degenerate than in the mature. The differential effect on the fronds is brought out in the comparison between the height of intact fronds only (Table 7) and the whole populations respectively (Table 8). As a matter of interest and as possibly affecting frond dimensions the percentage of fronds whose petioles were attacked by the larva of *Chirosia* sp. is given in Table 7.

Thus it comes about that with the lamina immature and/or crippled by frost, its length (and of course, height) is less than normal and the corresponding ratios lower especially in the pioneer and degenerate phases. But the values for petiole and total petiole will be unaffected.

It is also to be expected that substitute fronds fed from reduced reserves will be smaller. Exactly how the proportions of their parts are affected is not known, but total

petiole at least must be entirely dependent on reserves, while the lamina may be partly dependent on reserves and partly on the food made by itself. In a favourable growing season (as was 1940 with 2·83 in. of rainfall in July) the lamina may well be relatively longer. Thus in the relatively intact fronds in the building and mature phases the length of the lamina is relatively greater and of total petiole relatively less than in comparable zones in the margin (cf. the percentage data in Tables 3 and 8): the resulting lamina/total petiole ratio is high. It may be added that most of the adventitious fronds in pioneer and building whether of deep or moderately deep origin simulate pioneers in the shortness of the petiole.

A study of depth is illuminating both in emphasizing resemblances and in explaining

Table 9. *The percentage distribution of depth classes in the marginal population and in the hinterland: also in partial populations of these. The coefficients of variation for depth are also given*

Depth class	0–0·9	1–1·9	2–2·9	3–3·9	4–4·9	5–5·9	6–6·9	7–7·9	8–8·9	9–9·9	10–10·9	Coefficient of variation
Marginal plant, transect 0–80 ft.: 142 fronds	—	1·4	15·5	28·2	23·2	13·4	9·2	5·6	2·1	0·7	0·7	—
Near hinterland, transect 81–115 ft.: 50 fronds	—	6·0	30·0	38·0	16·0	10·0	—	—	—	—	—	—
Remote hinterland: 50 fronds	4·0	16·0	26·0	30·0	20·0	4·0	—	—	—	—	—	—
Marginal plant:												
Transect 0–20 ft., 21 fronds	—	—	—	—	14·3	9·5	28·5	23·8	14·3	4·8	4·8	4·843
Transect 21–40 ft., 41 fronds	—	2·4	14·7	29·3	26·8	19·5	4·9	2·4	—	—	—	4·407
Transect 41–60 ft., 40 fronds	—	—	32·5	45·0	15·0	5·0	2·5	—	—	—	—	4·741
Transect 61–80 ft., 40 fronds	—	2·5	7·5	25·0	32·5	17·5	10·0	5·0	—	—	—	4·900
At 0–11 ft., 50 fronds	—	—	—	—	4·0	24·0	36·0	16·0	16·0	2·0	2·0	2·601
At 20–30 ft., 50 fronds	—	—	8·0	26·0	36·0	20·0	8·0	2·0	—	—	—	3·674
At 40–50 ft., 50 fronds	—	8·0	32·0	44·0	10·0	4·0	2·0	—	—	—	—	4·495
Hinterland, 1940:												
Pioneer phase, 22 fronds	—	—	—	4·6	13·6	27·2	18·2	22·7	9·1	0·0	4·6	5·719
Building phase, 49 fronds	—	2·0	8·2	20·4	28·6	24·5	12·2	4·1	—	—	—	4·142
Mature phase, 39 fronds	—	10·3	41·0	35·9	7·7	5·1	—	—	—	—	—	5·484
Degenerate phase, 45 fronds	2·2	6·7	20·0	22·2	17·8	11·1	6·7	8·9	4·4	—	—	6·955

some differences. Data for the distribution of depth classes (Table 9) are given for four successive zones of the whole transect as well as for batches of 50 fronds from 0–11, 20–30 and 40–50 ft. (This set may be completed by using the data from the 61–80 ft. section of the transect.) Both sets from the marginal plant show a progressive shift upwards in the position or the magnitude of the mode for depth from the forward margin to the 41–60 ft. section: thereafter in the 61–80 ft. section the mode recedes. A similar sequence characterizes the four phases (vide also Fig. 4). The positions of the mode do not always coincide but the similar drift establishes the essential identity of the process of change in the four phases with the change across the marginal belt.

In the distribution of depth classes there is a further resemblance, for the values of the coefficient of variation (Table 9) show the same general drift (except for the batch of 50 from 0 to 11 ft. concerning which see the comment in Pt. II, p. 113).

The mean values for depth suggest that the fronds from the phases are older than those from corresponding parts of the transect. This is confirmed by the number of nodes (Table 8) which not only shows the expected sequence of change but are all higher than the corresponding values from the marginal belt at Red Lodge (Table 4). The explanation of this difference is found in the short shoots. In the sample from near the end of the
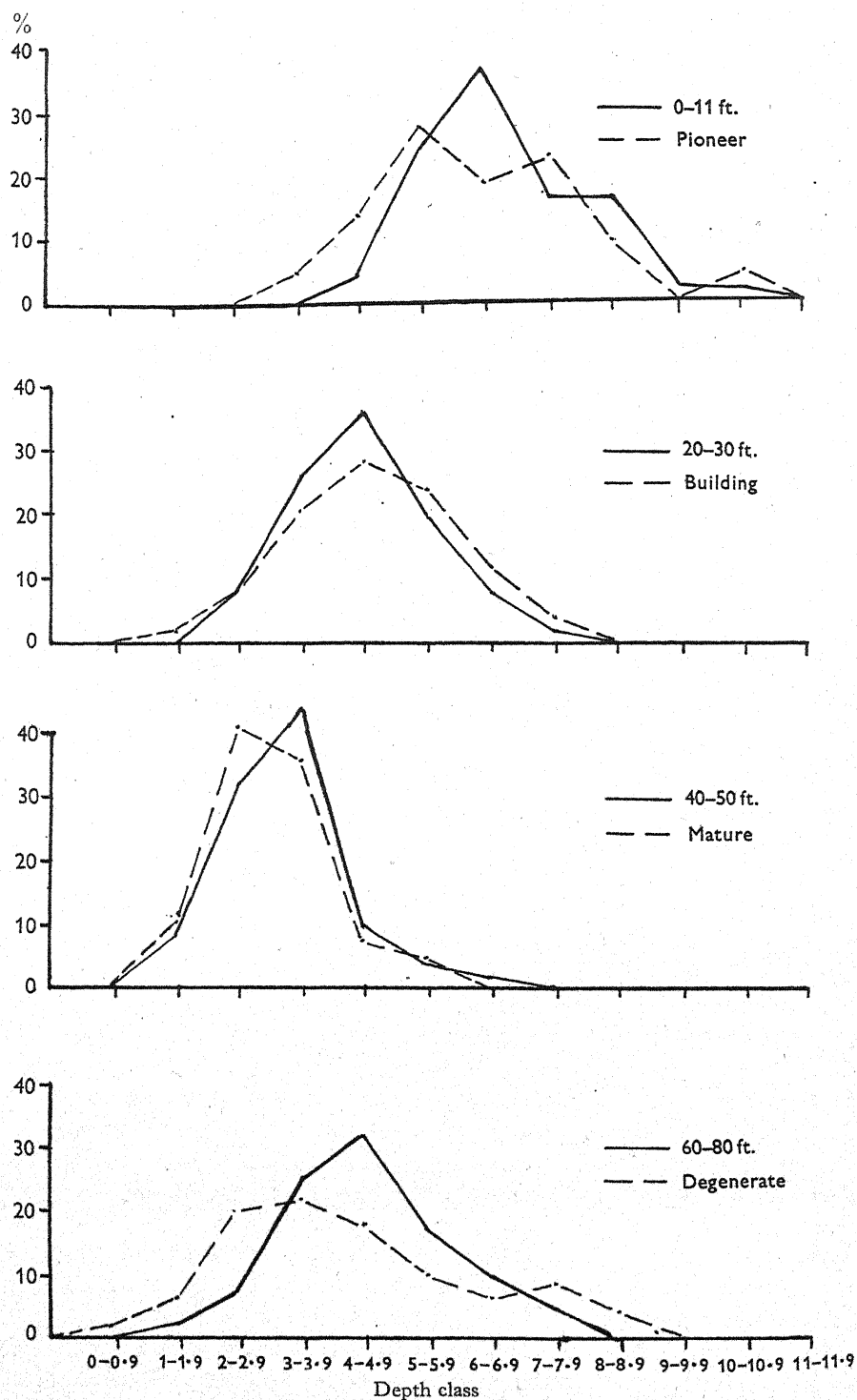
Fig. 4. Comparison between the percentage distribution of depth classes in partial populations
of the margin and four phases in the hinterland.

marginal plant at Red Lodge, branching of the short shoot is uncommon—no more than 6% of the fronds arise from branching shoots. The records do not make it clear in just how many branching followed the dying back of the apex, but in some at least this is believed to be so (cf. Watt, 1940, Pt. I, Fig. 6c). (This figure of 6% is not an estimate of shoots which have died back, but only of those which had died back and produced adventitious fronds.) If we assume this to happen in all then no more than 6% of the fronds are adventitious. In the hinterland of area E branching is common: approximately half of the fronds in each phase arise from branches of the short shoot of the first or second order. This is taken as meaning that in all phases in the hinterland there is a high percentage of adventitious fronds with the characteristics of older fronds (as indeed they are since they arise from old parts of the plant): and the origin of these fronds from relict
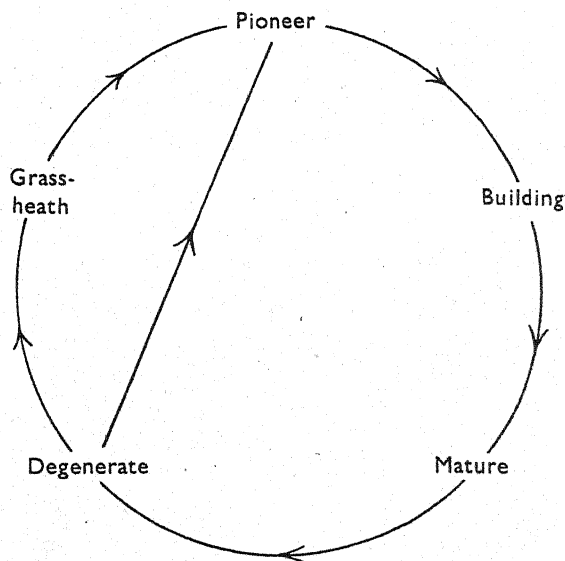
Fig. 5. Diagrammatic representation of the relation between the phases in the dynamic pattern of the hinterland population.

shoots is in general shallower than from true pioneers. Hence the lower mean depth. Since a low mean characterizes the population as a whole (p. 167) it follows that the number of fronds of the type found in the mature phase preponderate over those of deep origin. A subsidiary point worthy of note is that more short shoots in the hinterland reach a greater age than in the marginal plant.

The full significance of these facts becomes clear on the formulation of the hypothesis that the four phases form a cycle of change—a series in time at a given spot comparable with the space-time series in the marginal belt (Fig. 5). This accounts for the resemblances.

And it also accounts for the differences if regard is paid to the different conditions under which the plants live and move. The outpost fronds in the marginal belt enter soil free from bracken: in the hinterland, pioneers enter ground free from fronds (but not free from rhizome as the grass-heath phase always has some live rhizome in it, and it is known that the rhizome may lie dormant for some years without producing fronds) or the cycle is shortened by their entry into the degenerate phase. Further, stimulated by frost action, adventitious fronds from relict shoots may, and in these samples do, accompany

true pioneers in the pioneer phase: hence the shallower mean depth than that of the first 10 ft. section of the transect (Table 2) the greater number of nodes than in the 0–7 ft. sample from Red Lodge and the moderate coefficient of variation. Similarly the degenerate phase really consists of relics from the mature phase with their shallow origin and great age, adventitious fronds of deeper origin and a smaller number of true deep-set pioneers: hence the high mean number of nodes, the moderate depth and the fairly high coefficient of variation. These represent an intensification of the process of structural change already noted in the population from near the end of the marginal plant.

With the resemblances and differences in mind we may now briefly comment on the coefficients of variation and of correlation with depth. The effects of frost in the pioneer and degenerate phases render nugatory any useful comparison between these phases and their counterparts in the marginal population. Calculations of the values (as also of the means) for intact fronds only is a possible way out, which was dismissed because the number of intact fronds in the pioneer phase is too small (five only) and because its application to the degenerate phase would exclude a number of fronds highly characteristic of it. Because the building and mature phases are only slightly affected comparison is valid, as also are comparisons in the pioneer and degenerate between values involving petiole and total petiole which are unaffected by frost. Depth of origin has already been considered.

The coefficients of variation for petiole (Table 8) fall from a high value in the pioneer to a minimum in mature with a substantial rise in the degenerate. A similar fall in values is found in the marginal belt (Table 3) but there is no rise corresponding to the rise in the degenerate phase, not even when the values for 41–60 ft. (3·194) and for 61–80 ft. (2·658) are separately obtained. This difference is related to the greater variation in depth. The value of 14·82 in the pioneer compares with that of 13·14 for 0–10 ft. of the transect, but that for the building phase (5·958) is much less than either 11·07 (0–20 ft.) or 9·604 (11–20 ft.). On the other hand the value for the mature phase (4·341) is greater than that for 41–80 ft. (2·267) or than those (given above) for its two halves. Thus the building phase is less variable and the mature more variable than their marginal counterparts.

The values for the total petiole show a much narrower range with a general drift from pioneer to degenerate, the values for building and mature being similar. In the marginal population there is a similar drift even if the values for 41–60 and 61–80 ft. are considered separately (2·782 and 2·030 respectively). The value for the pioneer phase (5·245) is slightly less than that for 0–10 ft. (5·853): that for building (3·638) less than either 5·711 (11–20 ft.) or 5·631 (0–20 ft.) while that for mature (3·626) is greater than 1·770 (41–80 ft.) or its two halves. Once again the building phase is less variable and the mature slightly more variable than for contrasted parts of the margin.

On the other hand the variability (both of petiole and total petiole) of the pioneer and the 0–10 ft. section is similar while that for degenerate is similar for total petiole but different for petiole from the values for the end of the marginal plant.

These results together with a consideration of the correlations with depth (Table 8) help us to be more precise about the make-up of the phasic populations. The most significant feature about these values is the positive and significant correlations between total petiole and depth in all phases: the values are highest in the pioneer and building, intermediate in degenerate and least in the mature phase. This means that each population is sufficiently uniform with regard to position to give a significant fall in total petiole with

age—a feature characterizing a circumscribed partial population from the margin. And if it is known that fronds in the pioneer phase do vary much in the parts of the plant from which they arise, the characters of those fronds are such as to resemble those relating to age. There is a similar mixture in the degenerate phase, this time emerging in the values, for the negative and significant value for petiole (-0.6030) suggests an effect of position comparable with the value of -0.6482 for the total correlation with depth in the 0–20 ft. zone and the positive and significant value for total petiole suggests an effect of age. The correspondence between building and mature and 0–20 ft. and 41–80 ft. respectively of the marginal plant is seen in the general similarity of the values to those for the partial correlations with depth (Table 3), that is, to a population uniform with respect to position and structure in the building, but varying in the mature reflecting changing structure and just sufficiently uniform in frond type to give a fall in total petiole with age.

Thus, by and large, the partial population (phases) of the hinterland have features which can be interpreted in terms of position and age (both are manifest in the degenerate phase, age is more important in the other three). The differences between them are those mainly characteristic of position. The relations between the phases can be explained on the hypothesis of a pattern in space whose aspects or phases form a sequence in time.

Summary

The relation of the parts of the frond and the ratios lamina/petiole and lamina/total petiole to position on the plant and to age of the short shoot is considered.

In general there is with position a rise to a maximum then a fall from it in lamina, petiole and total petiole. On the other hand lamina/total petiole shows a significant fall with position to the region of maximum height: thereafter the ratio remains constant. Lamina/petiole shows no significant relation with position.

At a narrowly circumscribed position on the plant (structure of the rhizome synusia remaining constant) there is in general a fall in the parts of the frond with age, the ratios remaining more or less constant.

On the basis of these relations, frond types from different positions are characterized and the results applied in a comparison between the make-up of the marginal population and that of the hinterland. It is found that the hinterland population consists mainly of old fronds, that is, fronds of the type found in the posterior part of the marginal plant. This forms part of the explanation of the reduction in size of the frond, although the major part of the fall from the margin to the hinterland is attributable to a fall in the size of the plant.

The distribution of the frond types in the marginal population shows, in successive narrow zones parallel to the invading outposts, a sequence of fronds of increasing morphological age, and of relatively uniform age within each zone: in the posterior part there are the beginnings of a change in structure which is completed in the hinterland, where all frond types are found but the old preponderate.

The arrangement of the fronds in the hinterland is different: the fronds are patchy and there is a tendency (stronger in some kinds of patches than in others) for fronds of a uniform type to be grouped together, forming phases or aspects of a spatial pattern. When these phases are placed in a certain order their frond types are found to be similar

(when allowance has been made for the effects of frost and the space available for coloniza-
tion by pioneer fronds is considered) to those in the sequence of zones in the marginal
population.

Since the frond types in the marginal population show a sequence in space and, at a
given place, a sequence in time, so the phases in the hinterland form a pattern whose
aspects (phases) form a sequence in time. The structure of the population in the hinterland
is thus shown to be interpretable on a dynamic basis.

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GAIN AND LOSS OF MOISTURE FROM SMALL SAMPLES OF MARSH VEGETATION

By F. BAYARD HORA

Botanical Department, The University of Reading

(With 2 figures in the text)

This paper describes an experiment designed to follow the course of gain of water from rainfall and the loss of water by evaporation from small isolated samples of marsh turf kept in pots. The principle involved, which is essentially that of the tank evaporimeter at Camden Square, London (see Bilham, 1934), was to maintain the samples of turf in a uniformly wet state by periodic additions of water to the pots whenever they began to dry out and removals when they began to flood. Records were kept of these additions and removals for over two years.
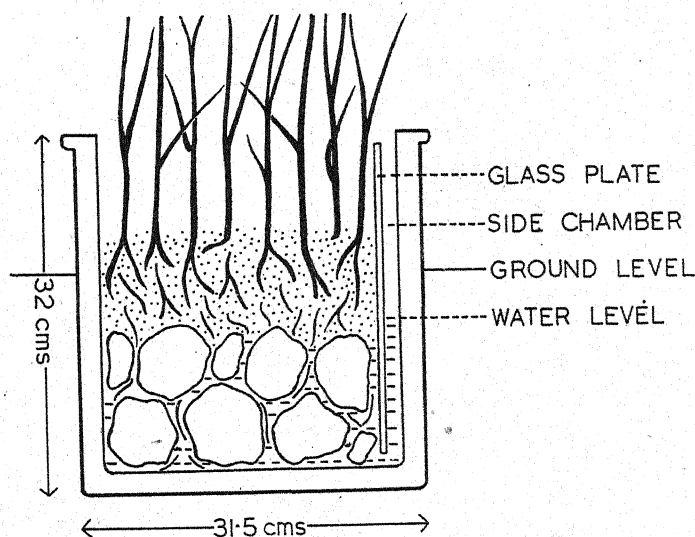
Fig. 1. Diagrammatic section through the experimental pot.

The apparatus consisted of six cylindrical pots and each was set up as shown in Fig. 1. The side-chamber was cut off as a small sector from the cylindrical pot by inserting a rectangular glass plate. In this way the water level in the pot could be observed and withdrawn by suction. The bottom of each pot was filled with stones (to a depth as shown) so as to make a water space, and live turf was placed on top, the soil surface being about 10 cm. below the rim of the pot.

The water-level was maintained at about half-way up the turf. Three pots were planted each with a *Molinia* tussock (*M. caerulea* Moench). This turf was obtained from Mortimer Common, Hants. The *p*H of the soil determined colorimetrically was 5·5. Three other pots were set up in the same way, but in each pot was placed a turf consisting almost

entirely of *Agrostis stolonifera* L., but with a few individual plants of *Poa pratensis* L. and *Agropyron repens* Beauv. This turf was obtained from a meadow by the calcareous Holybrook at Burghfield, Berks. Its *p*H determined colorimetrically was 7·5.

All six pots were sunk into the ground at the Reading University Botanic Gardens to within 8 cm. of each rim. They were placed in a line running due east and west, an *Agrostis* pot alternating with a *Molinia* pot, there being 60 cm. between each pot and the next. The ground sloped gently northwards and was fully exposed to sunshine, wind, etc., but there may have been some slight sheltering from a belt of trees (mostly elms) which also ran east and west about 30 yards to the north of the pots.

Whenever necessary, known amounts of rain water were added to the pots from a graduated cylinder to make up the level to about half-way up the soil, as judged by eye when looking down the side-chamber. Whenever the water-level rose during wet spells the excess water was removed and measured. These amounts of additions and withdrawals were recorded.

In the first year of the experiment nothing but rain water was added to make up any loss. In October 1942 tap water was substituted, and at the same time a generous supply of nutrient inorganic salts was added to two *Agrostis* and two *Molinia* pots in which the leaves appeared starved. The remaining two pots, one with each kind of turf, were left unmanured as controls.

It is difficult to adjust the water-level accurately, more especially when water is withdrawn as, owing to drainage, an uncertain and variable time is required for the water-levels in the turf and side-chamber to become equal. Accordingly, individual readings are not very accurate. However, over a long period, such as a year, this is of no importance, the cumulative errors of individual readings tending to cancel one another out. The error was, in fact, shown to be a statistically negligible fraction of the total volumes concerned.

The necessary data for rainfall (required to estimate total evaporation loss from the pots) were available at the University grounds less than a quarter of a mile away. They were obtained from a rain gauge of standard pattern 5 in. in diameter, readings being taken every morning. An experiment was carried out with one of the experimental pots placed close to this rain gauge, and it was found after a sharp downpour of rain both had received 0·48 in. of rain (the calculation for the pot being made on its internal diameter).

In the experimental pots rainfall is practically the only means whereby they gain water. However, in the early part of 1942 there was a short fall of snow which lay on the pots for some weeks. Meteorologists are familiar with the difficulties in recording moisture from snow. In the case of the experimental pots the results show that these take more water as snow than does the rain gauge, but since the total amount of moisture concerned as snow is relatively minute, this discrepancy is negligible.

Adjustments of water-level to the pots were made as occasion arose. In dry summer months three additions a week were sometimes needed, whereas in winter months several weeks passed without any attention being required. After a heavy downpour it was necessary to remove water almost immediately.

Readings were begun on 4 October 1941 and ended 31 December 1943, but for convenience the results are presented for the 2-year period from 1 January 1942. The results considered are under the three headings of (1) water-level, (2) rainfall, and (3) total evaporation.
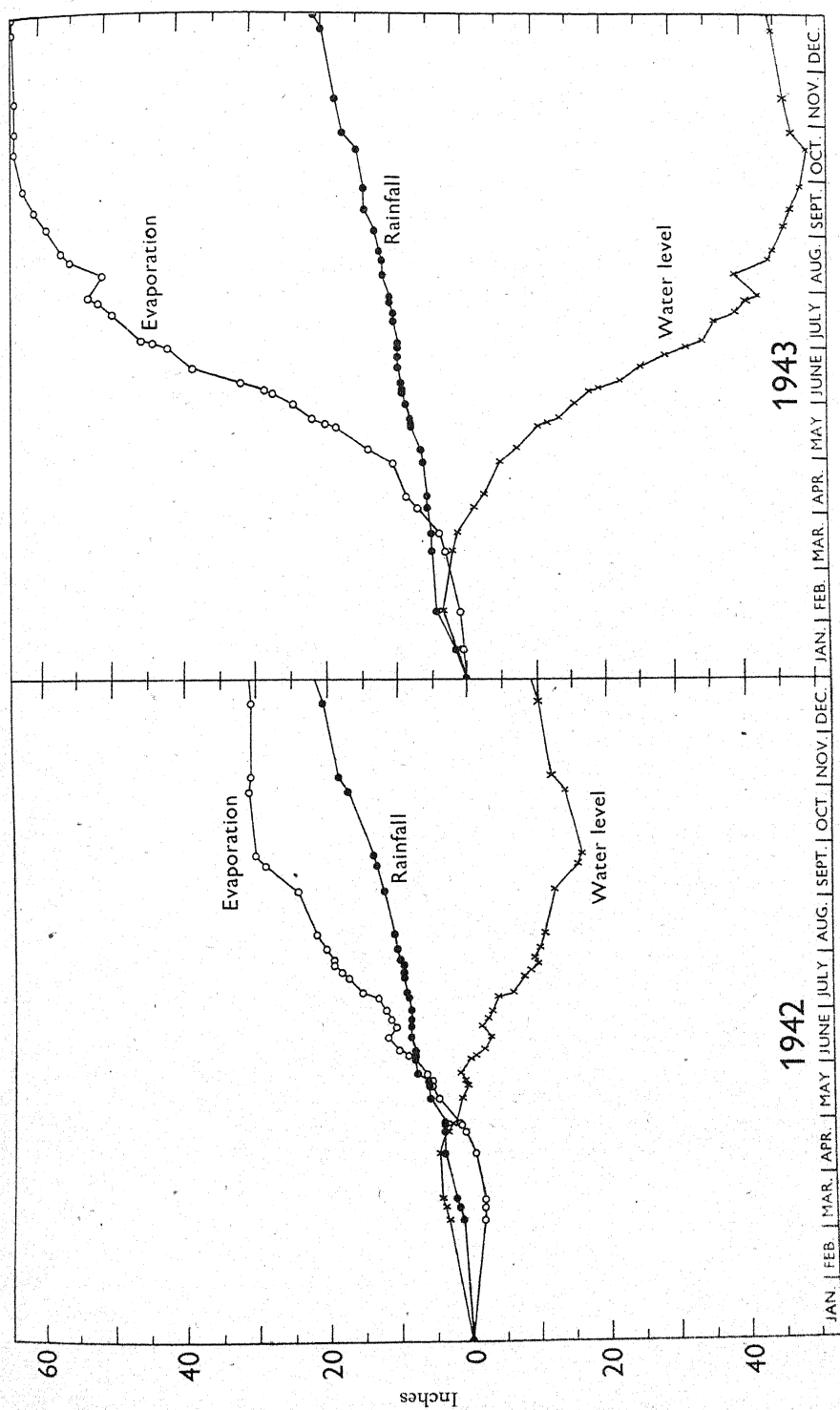
Fig. 2. Progress curves of the results of *Agrostis* 1 pot. For convenience, the results of the second year have been graphed as from zero. In actual fact, of course, the curves follow on continuously from the appropriate previous year's curves. The dip below the zero line in the total evaporation curve for 1942 is due to the experimental pot trapping more than its fair share of moisture as snow compared with the standard rain gauge.

The water-level graph is drawn as though it were the actual rise and fall of water-level (i.e. as it would have been without addition or subtraction of water by the experimenter), rain causing a rise, evaporation a fall. As stated above, water was added or removed periodically, and from the values for these adjustments the water-level progress curve was constructed. Thus, calling the level on 1 January 1943 zero, the pot was visited on 16 January when water had accumulated. This was removed and found to equal 2·37 in. of rain, and so 2·37 is graphed for the water-level on that date. On 6 February 1·97 in. of rain had accumulated: the total graphed is therefore 2·37 plus 1·97 = 4·34 in. Whenever water has been added, the graph of water-level has similarly gone down.

Rainfall data were summed for the same dates as adjustments to the water-level were made and also plotted as a progress curve.

The progress curve for total evaporation has been obtained by taking the difference (rainfall − water-level). The values so obtained represent water lost from transpiring leaves, from the soil and from such water surfaces as were exposed during the experiment.

RESULTS AND DISCUSSION

All six pots gave curves of similar appearance, the differences being only those of relative amounts of water lost during the summer. For this reason, the progress curves for the 2-year period of one *Agrostis* pot (*Agrostis* 1) alone are given, but the more important data for all pots are summarized in Table 1. In considering these curves, it should be

Table 1

I. Rainfall. 1 January to 31 December inclusive:
    1942. 21·43 in.
    1943. 21·23 in.

II. Approximate dates of beginning and end periods of net water loss, i.e. when water must be added to the pots to maintain constant level:
    1942. For all six pots: 12 April to 25 September.
    1943. For all six pots: 6 February to 18 October.

III. Approximate dates of period of net water gain, i.e. when water accumulates in the pots and must be removed:
    1942–43. For all six pots: 25 September to 6 February.

IV. Amounts, in inches, of water lost during periods of net water loss:

	Agrostis			Molinia		
Pot no. ...	1	2	3	1	2	3
1942	20·97	18·52	13·90	15·09	13·79	15·39
1943	52·99 M	51·06 M	28·38	31·22 M	32·50 M	17·48

V. Amounts, in inches, of water removed from the pots during the period of net water gain:

1942–3	12·13	10·18	6·21	4·46	4·68	4·91

VI. Total evaporation, in inches, for the year from 1 January to 31 December inclusive:

1942	31·08	30·79	22·99	24·76	24·07	25·30
1943	64·76 M	63·70 M	42·55	41·79 M	44·29 M	28·04

M = Inorganic fertilizers added October 1942. See opposite.

noted that the rainfall for the two 12-month periods is practically the same: 21·43 in. in 1942 and 21·23 in. in 1943. Differences between the 2 years are therefore due to such causes as affect loss of moisture from the pots by evaporation. It is evident that the curves for 1943 are essentially the same as those for 1942, except that in 1943 there was more evaporation. Some of this increase was general. Thus from the table it is seen that the unmanured *Molinia* pot lost 3 in. more in the second year, the unmanured *Agrostis* 20 in. more. It is possible that this can be attributed entirely to establishment and

increased growth of the plants. In the manured *Molinia* pots, the loss increased by 17 and 20 in. respectively, and in both the manured *Agrostis* pots by 33 in. Most of this increase may be attributed to the very vigorous growth of the manured plants.

The most important conclusion to be drawn from the 2 years' results is that the total annual evaporation under the experimental conditions, including that of constant water supply, is much greater than the annual rainfall. This result would seem to be of potential importance in considering the vegetation of fens and marshes fed by drainage inflow. Results pointing to a similar conclusion have been reported from field experiments made by Godwin (1931) in fen vegetation. Working at Wicken Fen, which has about the same rainfall as Reading, Godwin showed that considerably more water is lost during summer by the marsh vegetation than is received as rain. The water-level in the peat therefore falls and water begins to soak into the fens from neighbouring ditches. In winter, however, the rain water accumulates, raises the water-level in the fen peat, and drains away by the ditches. Godwin's results do not show whether the volume of water supplied by the ditches in summer exceeds that lost in winter, but his graphs of water-level are remarkably like those given here.

Godwin also used an 'insert phytometer' which essentially resembles these sunk pots but was designed to give accurate readings over short periods. It is interesting to compare his graph for hourly measurements through a day with those given here for a year.

In applying the results of our experiment with small samples of marshland vegetation to marshland in the field, among other difficulties must be recognized those due to small size of the pots and the chance of marginal errors. As recorded above, an experiment with an empty pot did indeed prove that there is no appreciable difference from that calculated in their uptake of rain. When full of grass, however, which sends up leaves obliquely over the sides, no doubt more rain may be caught and no doubt also more water may be transpired. A further experiment is planned to lessen this error.

Table 1 summarizes the more important data for all six pots over the 2-year period. Manuring with inorganic fertilizers took place in October 1942. Results affected by this treatment are labelled M. Reference to the graph will make clear the periods of time indicated.

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ON PHOSPHORIC ESTERS IN BARLEY

By C. R. C. HEARD

University Department of Botany, Oxford

Preliminary measurements of phosphoric esters in barley seedlings were reported by Arney (1939). They revealed the presence in trichloracetic acid extracts of three main phosphate fractions—inorganic phosphate; 'labile esters', hydrolysed by N HCl at 100° C. in 7 min.; 'resistant esters', unaffected by mild hydrolysis. It was further shown (James & Arney, 1939) that these fractions could be significantly correlated with CO_2 emission over the first 7 days of seedling growth, and a tentative scheme for the role of phosphoric esters in barley respiration was put forward. This scheme has now been considerably amplified (see James & Bunting, 1941; and James, Heard & James, 1944).

Apart from Arney's preliminary work, much of the evidence for the role of phosphates in respiration comes from experiments in which phosphoric esters have been added to barley saps or other preparations and measurements recorded of increased CO_2 emission, pyruvic acid formation, or ascorbic acid oxidase activity. It was obviously desirable to parallel these investigations with actual measurements of phosphates in the preparations. This has been done (James, Heard & James, 1944) and circumstantial evidence confirmed by direct phosphate analysis.

The present paper describes in more detail the methods of analysis used and the results of applying them to fresh plant material, Arney's results have been confirmed and extended, and a fuller picture of the phosphoric compounds actually present in the normal plant is now available.

MATERIAL

Barley, var. Plumage Archer, was used throughout. Seeds were soaked in water for 4 or 5 hr. at room temperature and then spread on wet muslin stretched over a dish of water and kept moist by capillarity in an incubator at 21° C. When the seedlings were 7 days old they were cut off above the grain and used in the experiments. A few analyses were also made of young green leaves from plants grown under natural conditions.

METHODS

The work of Lohmann & Meyerhof on the rates of hydrolysis of phosphoric esters provided the basis for the methods employed.

They have shown that if a tissue extract or mixed ester solution is adjusted to contain N HCl or H_2SO_4 and hydrolysed in a water bath at 100° C.:

In 7 min. adenyl pyrophosphate yields completely adenylic acid and two free phosphate radicals (Lohmann 1932);

and *triosephosphate* loses 44 % of its phosphate (Lohmann & Meyerhof, 1934a).

In 60 min. phosphopyruvic acid is completely hydrolysed to pyruvic acid and free phosphate (Lohmann & Meyerhof, 1934b);

and *triosephosphate* is also completely hydrolysed (Lohmann & Meyerhof, 1934a).

In 180 *min. hexosediphosphate* will lose 94 % of its second phosphate radical yielding hexose-6-phosphate;

hexose-6-phosphate will lose 22·7 % of its total phosphate (Lohmann, 1928).

If the extract is adjusted to N with NaOH and allowed to stand at room temperature 20° C. for 20 min., triosephosphate is completely hydrolysed (Lohmann & Meyerhof, 1934a).

In each case measurement of the inorganic phosphate present in solution before and after hydrolysis gives the extent of phosphate liberation and hence a measure of the corresponding phosphoric esters present in the extracts.

Conventions used in recording results

In the present paper and also in a preceding one (James *et al.* 1944), the following conventions were observed in recording results:

P_i = inorganic phosphorus content of unhydrolysed extract.

P_T = total phosphorus content of extract.

P_A = phosphorus liberated in inorganic form by 20 min. alkali hydrolysis.

P_7 = phosphorus liberated by 7 min. acid hydrolysis. 44 % of any P_A fraction would have to be deducted from the observed increase in inorganic phosphorus after hydrolysis. In the analyses recorded in this paper P_A was never significant and, therefore, P_7 represents the observed increase on 7 min. acid hydrolysis and is equivalent to Arney's 'labile ester' fraction.

P_{60} = phosphorus liberated by 60 min. acid hydrolysis. The P_7 and P_A values must be deducted from the observed value.

P_{180} = phosphorus liberated by 180 min. acid hydrolysis and not by 60 min. hydrolysis.

P_u = unhydrolysable esters or those whose phosphorus is completely liberated only on incineration; $= P_T - P_{180}$.

Therefore P_7 would include any adenyl pyrophosphate, if present; P_A any triosephosphate and P_{60} any phosphopyruvate. P_{180} would include the bulk of the hexosediphosphate, but also an appreciable amount of hexose-6-phosphate. Macfarlane (1939) multiplies the observed P_{180} value by 3/2 to give total hexosediphosphate phosphorus. Such corrections are valid only in a mixture of pure substances in solution, but it has already been shown (James *et al.* 1944) that, while pure hexosediphosphate solution is hydrolysed according to the manner described by Lohmann & Meyerhof, the presence of plant extract has a marked catalytic effect on the hydrolysis of hexosediphosphate. It was decided, therefore, to leave the P_{180} and P_u values as observed. In interpreting results it was reasonable to assume that if P_{180} were large compared with P_u, hexosediphosphate was likely to be the chief hexose ester; and if P_u were large compared with P_{180}, hexose-6-phosphate was likely to predominate. Between the two extremes both would be possible.

Extraction of phosphates

Extraction was carried out with ice-cold trichloracetic acid, the seedlings being ground with washed sand to a fine pulp and, after centrifuging, re-extracted and washed with a little more acid. The combined clear solutions were neutralized with NaOH (Analar)

solution and made up to volume with ice-cold distilled water. Normally 80–100 seedlings of average height were used, extracted with a total volume of 100 ml. 7·5 % trichloracetic acid and the neutralized solution made to 250 ml. In a refrigerator the solution may be kept for at least a week without increase in inorganic phosphate content. 5 or 10 ml. aliquots were diluted to 50 ml. before and after hydrolysis for phosphorus estimation.

The estimation of inorganic phosphate

Arney had to resort to a preliminary separation of the inorganic phosphate to avoid a yellow interference, using Fisk & Subbarow's colorimetric method. In the present work Berenblum & Chain's (1938) modification was used throughout and, as shown in Table 1, could be applied directly to the plant extract with the same results as were obtained by calcium precipitation, provided that the solutions were kept cool with ice. At room temperature some hydrolysis occurred during the calcium precipitation, liberating extra phosphate.

Table 1

Exp.	Inorganic phosphorus γ/seedling		Temperature of precipitation, etc.
	Direct estimation	After calcium precipitation	
16	42	52	Room
26	44	44	Ice
30	34	43	Room
31	39	39	Ice

The blue solutions were measured in a spectrophotometer, using an orange filter and, later, with increased accuracy, in a Spekker absorptiometer. Phosphorus concentrations were read off from calibration curves prepared from standard solutions of Analar KH_2PO_4 dried to constant weight at 100° C. Normally, the extract was diluted to give an inorganic phosphorus content of 20–40 γ P/10 ml.

Hydrolysis

Solutions of 2·0 N HCl or H_2SO_4 (Analar) and 2·0 N NaOH (Analar) were used and added in equal volume to an aliquot (5 ml.) of the extract. After hydrolysis the solutions were neutralized, cooled rapidly, and made up to 50 ml. and 10 ml. taken for analysis. Solutions were kept in a refrigerator until analysed.

(i) *Alkali hydrolysis*. The solutions were allowed to stand in conical flasks at room temperature for 20 min.

(ii) *7 min. acid hydrolysis*. Conical flasks containing the solutions were suspended in boiling water for 7 min.

(iii) *60 and 180 min. acid hydrolysis*. In the experiments quoted in this paper, conical flasks were used fitted with air condensers of 20 × 0·5 cm. glass tubing. Later, sealed glass bulbs were used and gave much more consistent results. Glass tubing about 15 cm. long and 1 cm. in diameter was used, and a 3–4 cm. diameter bulb blown at one end. After sealing the tubing, the bulb containing the solution was immersed in boiling water. When hydrolysis was completed, the tube was rapidly cooled, opened near the sealed end, and the contents washed out for analysis. Each bulb could thus be used for several analyses.

Total acid-soluble phosphate

For each test 2·0 ml. of the extract and 5·0 ml. of the 60 % perchloric acid (Analar) were boiled over a flame in a Kjeldahl flask covered by a cap connected with a filter pump to remove fumes. When a clear, colourless solution was obtained it was cooled, diluted, neutralized and made up to a convenient volume, e.g. 50 ml., and analysed.

In no case was the addition of H_2O_2 necessary to complete incineration, as it is when H_2SO_4 is used. Further, it was found that incineration with H_2SO_4 and H_2O_2 produced a considerable colour due to the reagents themselves whereas perchloric acid gave no blue. Neutralization must be carried out with NaOH (Analar) as other grades give a slight additional blue colour.

Table 2

Exp.	P in γ/seedling or leaf				
	P_i	P_7	P_{180}	P_u	P_T
26	44	7	0	13	64
29	34	2	0	11	47
30	34	9	7	43	93
31	39	7	—	—	—
35	39	0	4	39	82
36	49	6	2	4	61
37	31	1	2	2	36
Arney	22	4	—	34	60
Arney	26	1	—	37	64
32 (green leaves)	88	—	8	26	122

Table 3

Exp.	P % total phosphorus			
	P_i	P_7	P_{180}	P_u
26	69	11	0	20
29	72	5	0	23
30	37	10	7	46
35	48	0	5	48
36	80	10	3	7
37	86	3	6	6
Arney	37	7	—	57
Arney	40	2	—	58
Arney	75	3	—	22
32 (green leaves)	72	—	7	21

RESULTS

A number of experiments were performed on 7-day-old barley seedlings grown in the dark. Extraction, hydrolysis and analysis were carried out as described. Similar analyses were performed in the course of later experiments on green leaves, and the same methods were used in the sap analyses quoted in the previous paper (James *et al.* 1944). In fresh extracts of seedlings there were no appreciable P_A and P_{60} fractions which do not, therefore, appear in the results shown in Tables 2 and 3.

DISCUSSION

The total phosphorus present in the trichloracetic acid extracts remained fairly constant in the etiolated barley seedlings at between 0·05 and 0·10 mg. phosphorus per seedling top and agreed with Arney's figures.

Inorganic phosphorus

Of the total phosphorus some 70 % is usually present in the form of directly estimable inorganic phosphate. This applies equally to green leaves and etiolated seedlings. It introduced practical as well as theoretical difficulties, since the measurement of organic esters by hydrolysis methods depends on detecting a small increase in a large inorganic phosphorus fraction. Nevertheless, with care, consistent results can be obtained.

'Labile' esters

Although the amount varies (from 0 to 10 % of the total phosphorus) there is usually a fraction hydrolysed by the 7 min. acid treatment. This confirms Arney's results. Triosephosphate is not present in measurable quantity and cannot, therefore, be confused with the P_7 fraction. The phosphorus liberated by a further 1–3 hr. hydrolysis is seldom as great as that liberated in 7 min. Further, in estimating inorganic phosphorus by calcium precipitation in alkaline solution, and analysing the redissolved precipitate, it was found that, unless all these operations were carried out at ice-cold temperatures, inorganic phosphorus estimated in this way was greater than that estimated directly in the original extract by an amount exactly equal to the P_7 fraction; e.g. compare Exp. 30 in Tables 1 and 2. James *et al.* (1941) have shown, further, that adenylic acid can play a role in promoting barley respiration. It is, therefore, probable that our P_7 fraction indicates the presence of adenyl pyrophosphate, or some very similar ester, in barley extracts.

'Resistant' esters

About 20 % of the total acid-soluble phosphorus fell into the fraction resistant to 7 min. acid hydrolysis. Occasionally this fraction accounted for 50 % of the total, and inorganic phosphorus showed a correspondingly lower value.

Such variation has been shown by Arney to be related to CO_2 emission, increased emission being associated with increase in esterified phosphate and decrease in inorganic phosphate. It appeared that the combination of phosphate in ester form was a prerequisite of stimulated CO_2 output. Other workers (Bodnar, 1916; Jones, 1936) have shown that increasing the supply of inorganic phosphate increased plant respiration; and Tanko (1936), by adding inorganic phosphate to a pea preparation, isolated a mixture of hexosedi- and monophosphates. Normally, barley does not respond to added inorganic phosphate at this stage of growth, since the seedlings already have a sufficient content of inorganic phosphate to draw on for their maximal rates of phosphorylation and respiration. If, however, they were deprived of their normal endospermic reserves a response to external phosphate additions was observed (James & Arney, 1939).

The inference was clear that the 'resistant' esters, products of phosphorylation, had a close connexion with respiration. From the analogy of yeast, muscle and liver, hexosedi- and monophosphates were probably components of the resistant fraction in barley. Burkard & Neuberg (1934) showed the formation of glucose and fructose monophosphate in beet leaves. Hassid (1938) isolated a mixture of glucose and fructose phosphoric esters from pea leaves. In addition, it has been shown that plant material was capable of converting hexosediphosphate into phosphoric esters similar to those formed in yeast (Neuberg & Kobel, 1930, 1934*a*; Baba, 1935; Allen, 1938) and also of converting phosphoglyceric acid into pyruvic acid (Neuberg & Kobel, 1934*b*).

It was therefore a reasonable first step in trying to discover whether similar systems and compounds existed in barley to subdivide Arney's 'resistant' fraction into P_4, P_{60}, P_{180}, and P_u fractions as defined in this paper. This would reveal the presence of any measurable quantity of triosephosphate, phosphopyruvate, hexosediphosphate and hexose-6-phosphate respectively.

No triosephosphate was detectable in any of the extracts of fresh material. Phosphoglycerate, if present, would be represented in the P_u fraction, but Arney had shown that calcium precipitation does not decrease the resistant fraction which is left in solution, thus ruling out phosphoglycerate. It has been shown that pyruvic acid is not present in measurable quantity in fresh barley seedlings (James *et al.* 1941; James, G. M. & James, W. O. 1940). It was, therefore, surprising to find in the first three experiments recorded in Table 2 a small P_{60} fraction suggesting the presence of detectable amounts of phosphopyruvate. In the same experiment P_{180} gave negative values approximately equal to the P_{60} fractions. It has already been reported (James *et al.* 1944) that hexosediphosphate is much more rapidly hydrolysed by acid in the presence of plant extracts than in the pure state. The subdivision of the P_{180} fraction into separate P_{60} and P_{180} fractions was therefore abandoned and the recorded P_{180} values represent the phosphorus released by hydrolysis between 7 and 180 min. The values obtained were usually so small in comparison with the P_u values as to leave little doubt that neither phosphopyruvate nor hexosediphosphate could be present in significant amounts, and that virtually the sole component of the 'resistant' fraction must be hexose-6-phosphate, whose partial hydrolysis could easily account for the P_{180} fraction.

This is consistent with the fact that isolations from plant material have generally been of hexosemonophosphates; the rapid rate with which barley preparations dispose of hexosediphosphate; and the rapid consumption of sugar occurring at this stage in barley respiration when the more 'active' hexosediphosphate would have but a transitory existence compared with the monophosphate.

The results recorded here can give only a static picture of the distribution of phosphorus in barley seedlings; i.e. they show only the 'reserves' of the mechanism, or those compounds which temporarily accumulate, viz. inorganic phosphate, hexosemonophosphate and probably adenylpyrophosphate in the P_7 fraction. Other fractions which do not accumulate sufficiently to be estimated, e.g. triosephosphate, may yet occur transiently and must be sought by other means (see James *et al.* 1944).

SUMMARY

1. Trichloracetic acid extracts of 7-day-old etiolated barley seedlings were analysed for a number of phosphorus fractions. The total soluble phosphate averaged 0·064 mg. phosphorus per seedling shoot.

2. The extracts were hydrolysed in N HCl for 7, 60 and 180 min. at 100° C. and in N NaOH for 20 min. at 20° C. and the inorganic phosphorus content measured before and after hydrolysis.

3. About 90 % of the total phosphorus was contributed by inorganic phosphate and phosphoric esters not hydrolysed in 180 min. The proportion contributed by each of these fractions varied greatly, but normally inorganic phosphorus was the greater.

4. The fraction of the phosphorus liberated by 180 min., but not by 7 min. hydrolysis was of doubtful significance and seemed in general to vary according to the size of the unhydrolysable fraction. Reasons are given for supposing that the 180 min. fraction does not represent a distinct ester, such as hexosediphosphate, but results from partial hydrolysis of hexose-6-phosphate, the probable constituent of the unhydrolysable fraction.

5. Triosephosphate and phosphopyruvate were not present in measurable amounts.

6. An average of 6 % of the total phosphorus was released by 7 min. hydrolysis. It could be precipitated by calcium in alkaline solution and is regarded as a distinct fraction, probably adenylpyrophosphate or some similar phosphate carrier.

7. The results are discussed in the light of isolations of phosphoric esters from plant material reported by other workers, and of the role of phosphoric esters in barley respiration.

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A HISTOCHEMICAL STUDY OF THE DISTRIBUTION OF PHOSPHATASE IN PLANT TISSUES

By H. C. YIN

Sir William Dunn Institute of Biochemistry, and Botany School, Cambridge

I. INTRODUCTION

Much of the work on phosphatases has been done with animal materials. Similar enzymes have been demonstrated in plants. The commonest is the 'acid' phosphomonoesterase which hydrolyses hexose monophosphate, glycerophosphate and similar substrates with optimal activity at pH 5–6 (Folley & Kay, 1936). Young and actively growing tissues have been shown to contain large quantities of the enzyme. In a mature plant the highest activity is found in the leaves, a low activity in the stems, and a still lower in the roots (Ignatieff & Wasteneys, 1936).

With the advent of the histochemical method (Gomori, 1939) it is now possible to study the distribution of phosphatase in the different cells of the organism. A great deal of such work has been done on various animal tissues under both normal and pathological conditions (Glick, 1944). Only one paper has been concerned with plant material (Hilbe & Marron, 1940), and in this the authors reported that in germinating wheat the phosphatase is largely localized in the active part of the embryo and the cells immediately beneath the seed coat. It has been the aim of the present study to find a histochemical method more suitable for plant materials and to determine the distribution of the phosphatase in the various parts of the plant body.

II. PRELIMINARY EXPERIMENTS

Preliminary experiments have been made on a test-tube scale with expressed plant juice. The juice was incubated with sodium glycerophosphate in acetate-barbital buffers (Michaelis, 1931). The liberated inorganic phosphate was determined by the method of Allen (1940). The results showed that the optimal pH of the plant phosphatase is in the vicinity of pH 5. Activity decreases rapidly with increasing pH and practically disappears beyond pH 8 (Table 1). At the optimal pH the enzyme is not inhibited by iodoacetate ($M/500$), or cyanide ($M/500$) but is strongly inhibited by fluoride (75 % at $M/500$) (Table 2). The activity of the dialysed juice is not increased by the addition of magnesium salt ($M/1000$ $MgSO_4$) (Table 3).

III. MATERIALS AND METHODS

Two species of plants have been used, one dicotyledonous plant, *Lamium album*, and one monocotyledon, *Iris germanica*. Sections were made of the leaves, stems, roots and rhizomes. For the sake of comparison, some sections were also prepared from potato tubers and sprouts, cucumber stem and onion root. Freehand sections were generally used. They were fixed in 70 or 80 % alcohol for 3–5 hr., stepped down to water, incubated with reagents, washed, and mounted in glycerol. Sections made by the paraffin method have also been tried, but they showed much less phosphatase activity owing to destruction

of the enzyme. Improvement in fixation and embedding procedures will doubtless minimize this defect. In the present work, however, where comparatively thick sections containing intact cells are required, the freehand method of section cutting has been preferable.

The method of Gomori (1939) for the detection of phosphatase was first used. The method consists of incubating the tissue sections with glycerophosphate in the presence

Table 1. *Phosphatase activity of the expressed juice of* Lamium *leaves*

Mixtures made up of, 3 ml. diluted juice, 1 ml. sodium glycerophosphate (50 mg./ml.), and 5 ml. buffer. Incubation 1½ hr. at 30° C.

No.	Initial pH	Increase in inorganic phosphate μg. P/ml.
1	4	140
2	4·8	142
3	6	112
4	7	75
5	7·5	51
6	8·1	7
7	9	1

Table 2. *Effect of inhibitors on phosphatase activity*

Mixtures containing, 3 ml. diluted juice, 1 ml. sodium glycerophosphate (50 mg./ml.), 5 ml. buffer at pH 5, and 1 ml. $M/50$ inhibitor solution or water. Incubation, 1 hr. at 30° C.

No.	Inhibitor	Increase in inorganic phosphate μg. P/ml.
1	—	39
2	Na I.A.A.	39
3	KCN	36
4	NaF	10

Table 3. *Effect of magnesium on phosphatase activity*

Mixture containing, 3 ml. juice dialysed 18 hr. in distilled water, 1 ml. sodium glycerophosphate (50 mg./ml.), 5 ml. buffer at pH 5, and 1 ml. water or $M/100$ $MgSO_4$.

No.	Activator	Increase of inorganic phosphate μg. P/ml.
1	—	28
2	$MgSO_4$	29

of calcium nitrate. Inorganic phosphate freed by the action of the enzyme is immediately precipitated by calcium which is then replaced by cobalt. On treatment with ammonium sulphide a black precipitate of cobalt sulphide is formed in the vicinity of the enzyme. In general, the method gives a fairly good picture of the distribution of phosphatase as checked by the method given below, but it has the disadvantage of the interference caused by calcium and other insoluble salts originally present in the tissue. For this reason it is not suitable for plant tissues where calcium is always present and cannot be removed easily without damaging the enzyme. All sections have, therefore, to be studied against controls similarly treated but minus glycerophosphate. Such visual comparison is difficult and inaccurate.

To overcome this difficulty the method of Menton, Junge & Green (1943) has been used instead. According to this method the sections are incubated with naphthol phosphate* and α-naphthylamine diazotized with sodium nitrite. The free naphthol split off by phosphatase is precipitated *in situ* as an insoluble purplish red azo dye. In this way the interference of calcium or other salts is eliminated. The method was originally intended for the alkaline phosphatase of animal tissues and was used at pH 9–9·4. In the present work the reagents were brought to pH 6 and buffered at that pH with acetate-barbital mixture (Michaelis, 1931). Incubation lasted for 30–90 min. at a temperature of 4–6° C. to avoid secondary reactions.

A series of controls has been made with similar treatment but (1) without naphthol phosphate, (2) plus glutathione, (3) plus sodium fluoride ($M/300$),† (4) using boiled sections, and (5) at pH 9·2. None of these sections showed the characteristic purplish red colour which is therefore specific for the phosphatase. Two points should be mentioned here. One is the yellowish brown coloration in the boiled sections and in some sections which have been incubated for a longer time or at a higher temperature. It is due to secondary decomposition reactions (Menton *et al.* 1943) and has nothing to do with phosphatase. Second is the orange-red colour of the lignified cell wall of the fibre cells and some xylem vessels. It is apparently due to a reaction between the diazotized amine with some cell wall constituents as it also appears in sections to which the substrate, naphthol phosphate, has not been added or in which the enzyme activity has been inhibited by fluoride. Both colours are, however, easily distinguishable from the characteristic purplish red colour of the phosphatase reaction.

IV. Results

(1) *Leaf.* In the leaf the phosphatase activity is highest in the palisade chlorenchyma. In *Iris* leaves where there are several layers of palisade cells there is a gradual decrease of activity from the surface inward; no activity is found in the spongy parenchyma. Thin leaves like those of *Lamium* show activity in all the chlorenchyma, but lower in the spongy than in the palisade layer. The chloroplasts are more strongly stained than the cytoplasm, but it is not possible to determine whether the enzyme is concentrated in the chloroplasts themselves or in the surrounding cytoplasm at the interface with the chloroplasts.

The epidermal cells show practically no phosphatase reaction although the guard cells of *Iris* and the young epidermal hairs of *Lamium* give a positive reaction.

Among the conductive tissues the phloem elements give the most intense phosphatase reaction. The parenchyma cells in the veins and the sheath surrounding them are also rich in the enzyme. No activity is found in fibre cells and xylem vessels. In the small veins and vein endings the tracheids are inactive but the border parenchyma cells are active.

(2) *Stem.* No phosphatase activity is found in the epidermal cells except the basal cells of the young epidermal hairs (*Lamium*). Nor is the enzyme found in the corner collenchyma of *Lamium*, nor in mechanical tissues such as the scattered fibre cells of the potato sprout.

The outer layers of the cortical parenchyma which are normally green are high in phosphatase but the inner layers, normally colourless, show very little or no reaction.

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* Calcium salt, prepared by Dr J. F. Danielli.
† Some sections showed very faintly positive reaction due to incomplete inhibition.

The endodermis which is visible in some stems (*Lamium, Cucurbis*) is active. The pericyclic parenchyma, the medullary rays and the pith cells are all inactive.

In the vascular bundles the phloem is the most intense in phosphatase reaction. The cambium layer activity is less intense. The xylem elements are inactive except the parenchymatous cells which show fairly high reactivity. It is interesting here to note that among the phloem elements the companion cells are particularly strongly stained and in some sections a portion of highly stained cytoplasm is visible in the sieve tubes.

Intense phosphatase reaction is shown by the young stem. All the meristematic cells of the growing point are strongly stained. A little distance behind the apex, the staining becomes less intense in the inner cortex and pith but shows no decrease in the outer cortex and the procambium strands.

(3) *Roots*. Comparatively little phosphatase activity is shown by the root tissues. It is mostly confined to the central cylinder. In a mature root both the epidermis and the cortex are practically without activity. In the root hair zone the root hairs and the outer layers of cortex are slightly active. In the stele, phloem is again the most active tissue. The pericyclic parenchyma and the protoxylem cells are also active.

In the root tip and the primordia of secondary roots the whole meristematic tissue is highly active in phosphatase reaction. Only the cells of the root cap are devoid of activity. A little distance below the tip, where the primary zonal differentiation has begun, the cortical zone becomes less active while the procambial zone remains as active as the meristem.

(4) *Storage organs*. In sections of the potato tuber positive reaction is found in all cells except the periderm, i.e. in all cells where starch is stored, the cortex and the phloem-carrying parenchyma. The conductive cells are even richer in the enzyme. It is interesting to note that not only the phloem and the parenchyma but also the annular xylem vessels are fairly active.

A similar picture is found in the rhizome of *Iris* but the activity of the storage cells is very much less pronounced.

V. DISCUSSION

The present investigation shows that the various tissues of plants differ greatly in their phosphatase content. The highest activity is found in the meristematic cells, the chlorenchyma and the phloem tissues.

It is generally believed that phosphatase plays a part in cell metabolism. High phosphatase content is associated with active growth (Ignatieff & Wasteneys, 1936). The intense reaction here shown by the meristematic tissues is consistent with this view.

Several hypotheses have been put forward as to the special functions of phosphatase in the higher animals. It has been suggested, for example, that it takes part in kidney secretion, intestinal absorption, lactation, and bone deposition (Folley & Kay, 1935). Apparently it plays a rôle in carbohydrate transformation and secretion. The present finding that phosphatase is concentrated in the phloem elements and the bundle parenchyma is of interest in this connection. These tissues have been proved to be the channel of transportation of organic materials and of phosphorus compounds (Biddulph & Markle, 1944) in plants. There is a positive concentration gradient of sucrose in the sieve tubes of the leaves and the stem (Mason & Maskell, 1928). According to Phillis & Mason (1933) the border parenchyma and the companion cells have a secretory or accumulatory function

in that they bring about sugar transformations which build up the concentration gradient. Since these cells are especially rich in phosphatase it is likely that this enzyme is involved in these carbohydrate transformations. The results of physiological studies on sugar cane (Hartt, 1943, 1944) and of infiltration experiments on leaves (Kursanov & Kryukova, 1940) are in accordance with this view.

The fact that phosphatase is present in large amount in the chlorophyllous cells does not necessarily mean that the enzyme is concerned directly in photosynthesis. Although it has been suggested on theoretical grounds that phosphorylation reactions are involved in photosynthesis (Ruben, 1943) there is so far no satisfactory experimental evidence. Analyses of various phosphate fractions of plant tissues in light and in darkness have as yet produced no definite result (Barrenscheen & Pany, 1930; Cockefair, 1931; Emerson, Stauffer & Umbreit, 1944). Unpublished data obtained in the course of the present investigation have shown that analytical results of phosphate fractions in plants are quite variable and difficult to interpret. It is quite possible that here the phosphatase is mainly concerned with carbohydrate transformations as it is in the conductive elements.

VI. SUMMARY

1. The histochemical method of Menton, Junge and Green for the determination of phosphatase is used to study the distribution of the acid phosphatase in sections of plant parts.

2. High phosphatase activity is found in the meristematic tissues, the chlorophyllous cells and the phloem elements.

3. The possible role of phosphatase in plant metabolism is discussed.

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OBSERVATIONS ON SOIL ALGAE

I. THE ECOLOGY, SIZE AND TAXONOMY OF BRITISH SOIL DIATOMS

By J. W. G. LUND

Freshwater Biological Station, Wray Castle, Ambleside

(With 18 figures in the text)

PART 1

CONTENTS

A. INTRODUCTION

The term soil diatoms refers to those growing on soil moistened solely by direct atmospheric precipitation and is synonymous with Petersen's term eu-terrestrial (1935, p. 2).

British soil diatoms have received little attention, apart from Bristol's (1920) investigations,* and the present contribution is designed to enlarge our knowledge of this important group of soil algae. The taxonomy of soil diatoms, in particular, is in great need of clarification. It is frequently very difficult or impossible to decide what are the species discussed or described by previous workers. Some of the taxonomic tangles defy unravelling at the present time (e.g. *N. insociabilis*, Part 2), and a decision can only be reached by some future monographer. To this end direct observations have

* Many of my collections, especially those from cultivated soils, were made in the same area.

been made on sixty-six soils and have shown that, for the areas studied, the diatoms are more abundant than the Myxophyceae and about as abundant as the Chlorophyceae, except on acid soils (cf. Petersen's cultural results, 1932a, 1935). All cultural results by themselves are open to the objection that they favour hydroterrestrial (Petersen, 1935, p. 3) forms. The best are, probably, the moist cultures (John, 1942, pp. 325, 340), but even these tend to be unnaturally moist over long periods and should be combined with direct observations (cf. Petersen, 1928, p. 352).

B. MATERIAL

The samples, though collected from varied habitats and localities, did not include any as rich in calcium carbonate as the chalk soils of John (1942) or from sand-dunes. They can be grouped roughly into woodland and thicket (17 samples), moorland (4 samples), garden and allotment (27 samples), arable land (5 samples), paths and path verges (6 samples), grassland (3 samples), sand heaps (2 samples), burnt ground and rotted turf (1 sample each). The *p*H ranged from 3·7 to 8·3. For list see Part 2.

It is intended to consider the other elements of the algal flora in a further paper, though in less detail, since time did not permit of as close a study of the other groups.

C. METHODS

(i) *Collections*

These were not made during prolonged periods of drought or from soils that had been disturbed recently, in order, as far as possible, to eliminate these two factors as causes of the richness of the flora present. On the other hand, waterlogged soils or soils moistened other than by direct atmospheric precipitation were not examined, in order to exclude truly hydroterrestrial forms. Stokes (1940) found that the moisture content had a decided effect on the algal growth. There was an optimum range of 40–60% of the moisture-holding capacity of the soil. Excess moisture was less detrimental than suboptimum amounts, though the inimical effects of excess were particularly marked on surface-growing populations. It must be remembered, however, that there is no clear-cut margin between eu-terrestrial and hydroterrestrial habitats, since shaded soils may remain comparatively moist over long periods while hydroterrestrial habitats may dry up in periods of severe drought. Ground completely covered by vegetation was not examined. The aim was to study the normal flora of ordinary soils under reasonably favourable physical conditions.

Approximately the top 2 cm. were removed with a sterile knife or scalpel and placed in tobacco tins. Only the actual surface was examined in detail in all but one soil (see p. 207), but the complete slices of soil were used for the enriched (see below) samples so that any species living just below the surface would be included. Whenever possible, the soils were examined on the day of collection, but the majority were examined on the day following and some 2–3 days afterwards. Nine of the samples were not collected personally.

(ii) *Chemical analyses*

*p*H was determined colorimetrically, using a Lovibond comparator. Compared with electrometric methods this has the disadvantage that the more the soil solution is diluted and the further the *p*H is from that of the distilled water mixed with the soil (in the

ratio of $4:1$ by weight), the more the true pH is likely to be altered. Thus the more acid soils may have been really even more markedly acid.

Base deficiency was determined by Comber's method as modified by Misra (1938).

Prior to further analysis the soil was air dried, broken up in an agate mortar and passed through a 1 mm. mesh sieve.

Carbonate content (expressed as $CaCO_3$) was determined with a modified Collins calcimeter (to be described elsewhere); readily available phosphates by the method of Williams & Stewart (1941), the ratio of soil to $0.5\,N$ acetic acid being $1:100$; organic content by ignition at $650°$ C. and making allowance for the carbonate content; and the presence or absence of nitrates by Pearsall's (1938, p. 191) method.

Readily available potassium. I am indebted to Mr E. S. Twyman for this method, which is based on that of Wolf (1943) and has been found satisfactory for agricultural purposes. It is stated to give figures closely approximate to those obtained by the 1% citric acid estimation and to be accurate to about $\pm 10\%$. A Spekker absorptiometer is standardized to give a drum reading of 1.0 with distilled water. KCl standards containing equivalents of 5, 10, 15, 20 and 25 p.p.m. K_2O are made up in the extracting solution ($0.5\,N$ acetic acid) used and the absorptiometer calibrated by using the same procedure as given below for the soil samples.

The reagents used are: $0.5\,N$ acetic acid, ethyl alcohol and sodium cobaltinitrite. To make the last solution, 210 ml. of a solution of 120 g. sodium nitrite dissolved in 180 ml. distilled water are added to 25 g. of cobaltous nitrate in a solution of 12.5 ml. glacial acetic acid and 50 ml. distilled water. Air is drawn through the mixture until no more HNO_3 comes off. The sodium cobaltinitrite will keep at least 2 weeks in a darkened bottle.

100 ml. of $0.5\,N$ acetic acid are added to 10 g. of soil and the whole shaken at intervals during the day, the estimation being carried out the following morning after filtration through no. 3 Whatman paper. Since readings are affected by time and shaking, the following procedure must be carried out in the order and manner detailed for both standards and soil samples:

(1) Place 5 ml. of filtered soil extract (or standard) in a small bottle.

(2) Add 0.4 ml. sodium cobaltinitrite.

(3) Immediately add, with shaking, 5 ml. ethyl alcohol.

(4) Shake the whole for 1 min., leave in dark for 5 min., shake for a further 1 min. and read turbidity in a 1 cm. cell using the orange Spekker filters.

Carbonate, phosphate, organic matter and potassium contents are expressed as percentages of the dry weight found by heating a portion of the mixed soil at $105°$ C. All estimations were carried through in duplicate on the top 2 cm. of soil.

(iii) *Direct observations and cultures*

The sample was removed from the soil surface by scraping portions of the surface of the soil slices with a sharpened edge of a triangular needle. Mounts were made on seven slides under $1\frac{1}{2} \times \frac{7}{8}$ in. coverslips, as much soil being mixed with the sterile distilled water as possible without hindering microscopic observation. Using a $\times 10$ eyepiece and a $\frac{1}{6}$ in. objective, five longitudinal transects were made over each preparation. The diatoms present were noted and the unidentified specimens roughly drawn and measured. After examining a number of trial soils it was possible to separate and

identify many of the species in the living state, but this was always checked by examination of the cleaned frustule. Some of the species could not always be separated in the living state with certainty (e.g. *Navicula pseudagrestis*, *N. muralis* f. *agrestis* and *N. pseudatomus*; *N. cincta* var. *Heufleri* and *N. cryptocephala* f. *terrestris**) at the magnification used for direct observation, but the occasional dead frustules usually present sometimes made separation possible. An attempt was made to use the chromatophores as a basis for distinction, but these were frequently unclear at the magnification used and often more or less hidden by metabolic products. Sometimes forms with similar valve outlines could be differentiated by the robustness of the valves (e.g. the feebly silicified forms of *N. pseudatomus* from the fully silicified *N. seminulum*). A final computation was based on their relative abundance in the permanent mounts. These will contain some frustules from the previous flora but, usually, the majority of the dead frustules are soon washed away. Finally, a sixth transect was made under a $\frac{2}{3}$ in. objective and any further algae noted. The abundance was roughly computed by means of symbols (see p. 202), each one in ascending order being considered as representing an abundance approximately double that of the symbol below. Where two or more were equally abundant the dominant species were noted. Apart from the obvious inaccuracies of this method, it must be remembered that a few specimens of *Pinnularia viridis*, *Hantzschia amphioxus*, etc., are biologically equivalent to a number of *Navicula pseudatomus*, *N. minima*, etc. Nevertheless, the method was of considerable value in assessing the richness of the growth on the various soils (cf. the productivity numbers, p. 202). It should be realized further that only the common diatoms are observed and that even those forms listed as very rare may be present in considerable numbers per gram of surface soil.

The material from two of the preparations was run on to an agar plate (0·05 % Benecke solution in 2 % agar), from four of the slides into a cleaning mixture (see below), and the seventh slide placed in a moist chamber and examined from time to time for about a week. A further sample of soil was placed in a Petri dish and moistened with 0·05 % Benecke solution. These last samples are hereafter described as 'enriched samples'. On top of this soil were placed a number of no. 1 coverglasses sterilized by passing through a flame. The algae grew richly on the undersides of these coverglasses which could be removed and examined under oil immersion, if necessary, in spite of any adherent lumps of soil or sand grains. Alternatively, they could be turned into drop cultures or placed in a moist chamber. This method is of great value for examining members of the other algal groups. It has also the advantage that the position of any doubtful diatom can be fixed prior to incineration, and of enabling a large mass of diatoms to be removed from the sample with but little soil, greatly facilitating the subsequent cleaning and examination of the permanent preparations.

The cultures were examined, when possible, at approximately the following intervals: first fortnight, first, second and third months and thereafter at 2-monthly intervals for a year. The enriched samples proved the most valuable. A number of the cultures were lost by enemy action before any detailed examination of the diatoms was possible, and some of the soils, especially those not collected personally, were not cultured.

By restricting the cultures to small samples of the soil directly observed, the number of stray non-terrestrial species present was reduced to a minimum. This is of importance,

* For authorities, taxonomy of species and figures 2–18 mentioned in sections A–E, see Part 2.

since large lists of soil algae recorded by some workers (e.g. Fehér, 1936a, 1936b; Fehér & Frank, 1936; Killian & Fehér, 1939; Smith & Ellis, 1943; Gistl, 1931–2, 1933) contain many aquatic or semi-aquatic species. For this reason, too, moist or agar cultures are preferable to liquid cultures, since the latter provide conditions especially favourable for aquatic species, stray cells of which may multiply to such an extent as to crowd out the true soil species, these latter, perhaps, growing only slowly when totally submerged for prolonged periods. Where cultures were destroyed, slides were examined instead.

(iv) *Diatom preparations*

The soil containing the diatoms was boiled in a mixture of conc. HNO_3 and H_2SO_4 until the liquid became clear. Sometimes it was necessary to add a few crystals of KNO_3 to the boiling mixture to destroy all the organic matter, or some conc. HCl to render the iron soluble. After cooling and diluting with filtered tap water, the diatoms were washed on a hardened filter paper (Whatman's 541) until free of acid (testing with universal indicator), the tap water first running through a filter paper suspended above that containing the diatoms; thus no diatoms from the water supply became mixed with those from the soils.

The cleaned diatoms were mixed with filtered water and some of the suspension pipetted on to several no. 1 coverslips lying on the top of a 60° C. oven. The amount of suspension added must not be too great or the resultant preparation will be too opaque, nor must the suspension be dried at too great a heat, or the particles will clump together. When dry, the coverslip was inverted and mounted on a slide. Thus, the diatoms were fixed to the undersurface of the coverslip, and though sand grains might be present in the preparation, it was still possible to use oil-immersion objectives on it. Any attempt to make a preparation not containing sand grains results in the loss of some of the diatoms, especially the larger specimens.

In the case of coverslips from enriched samples (see above), either this method was used or they were placed on an iron plate and heated. If overheated the coverslip will buckle and both heating and cooling must be carried out by gentle stages to prevent the glass cracking.

Hyrax, methylene iodide (non-permanent) or a mixture of antimony bromide and piperine were used as mountants. For the latter, which has the highest refractive index, I am indebted to Dr R. W. Butcher. I have slightly altered his method of making the preparations. The coverslip and slide are placed on a hot plate at low heat, or warmed over a bunsen burner, and some of the piperine-bromide mixture placed on each; on melting, bubbles are evolved and when these cease, the coverslip is inverted and slid on to the slide. The cooled preparation is ringed and is then permanent (7-year-old slides are still in perfect condition). The bromide and piperine must first be finely powdered and not mixed until just prior to use. Once mixed they slowly react with one another and make very dark preparations. Mixing should be thorough, as the particles tend to clump together. The compounds are best kept in a desiccator. Dr Butcher advises 1 part of antimony bromide to 2 parts of piperine, but, as the former has the higher refractive index, I have used equal quantities or 2 parts of bromide to 1 part of piperine. The last proportion is not very satisfactory, as the mixture tends to become too dark on heating. These preparations are referred to hereafter as 'permanent mounts'.

(v) *Drawings and measurements*

In my figures I have, as far as possible, followed the methods of Hustedt (1930). The limitations of both drawings and photographs have been discussed by Voigt (1942). While a mountant of high refractive index is necessary in order to observe the striae, which are often especially faint in soil forms, one of low refractive index is best generally for cell outlines, hence the difficulty of drawing both with equal accuracy from one and the same specimen. I have further, as far as possible, made all the drawings at the same magnification, in order to facilitate comparison and differentiation of the species. This has one disadvantage, namely, that in the larger forms the three-dimensional form is more marked than in the smaller, where the distance in depth between the surface and the optical longitudinal section is hardly noticeable. Where the punctae of punctate forms are clear enough to be represented with accuracy (e.g. *Navicula mutica*) I have drawn them as separate dots. Where they are clearly present but not distinct enough to be so drawn, I have indicated them as dots along a continuous line (e.g. *Stauroneis Borrichii*). In some species the more central striae can be seen to be composed of separate dots and the more apical cannot be clearly so seen and the two sets have been represented differently (e.g. *S. montana*). Where they are not so clearly present I have represented them by continuous lines (e.g. *S. truncata*). In many of the species the more central striae are thicker and more prominent than the more apical ones and have been so indicated, but the difference may be so slight that it is impossible to represent it with complete accuracy. The different appearance given by different styles of drawing is well seen in *Navicula terrestris* (see Part 2, and compare the figures of Hustedt, 1924, fig. 8; 1930, fig. 477; Petersen, 1915, fig. 7; Bristol, 1920, text-fig. 8, figs. 15, 16; McCall, 1933, fig. 14*a* and those given here with the photograph of McCall, 1933, fig. 14*b*).

Measurements have been made to the nearest $1\,\mu$ in the larger forms and to the nearest $0 \cdot 5\,\mu$ in the smaller. Measurements can hardly be accurate to more than $\pm 1\,\mu$, but, in the small forms, smaller differences in size are, nevertheless, quite clear at the magnifications used. The calibration of both the ocular and stage micrometers was checked at two different times against two others. For the estimation of the density of the valve markings, see p. 214.

(vi) *Descriptions*

Hustedt's (1930) terminology, which I have used, differs from that of Bristol (1920) in that, to describe the direction of the striae, he uses the terms (1930, p. 228, fig. 345) parallel, radial and convergent (occasionally perpendicular instead of parallel in the text) where Bristol uses perpendicular, convergent (occasionally also radial) and divergent.

The following abbreviations are used: appr., approximately; br., broad; c.d., carinal dots; l., long; str., striae; S followed by a number or letter refers to the soils listed in the Appendix (e.g. S_3 = garden soil, Edgbaston).

D. ECOLOGY, GENERAL

It is difficult to make even tentative suggestions as to the chemical factors influencing the growth of soil diatoms in nature, since this is often controlled by the firmness of the surface of the soil, its water content over a period of time and the amount of shade.

The last is often seasonal, there being bare patches of earth in the spring (e.g. woods). Without a firm surface, the population will be depleted by any heavy shower, and I have observed a macroscopically visible growth completely disappear within 15 min. in a thunder shower. The configuration of the area was such that it was clear that the main part had passed into the soil. Similarly, after digging one-half of a plot, it took over 2 months before a new flora was formed on it which was as rich as that of the undug half. On sloping soils, however, heavy rain may wash off some of the surface growth.

(1) *Results of present investigation*

Fig. 1 illustrates the richness of the diatom flora on the surface of fifty-eight soils relative to readily available phosphates, nitrates, pH, base-deficiency and calcium carbonate. The data, which are not self-explanatory, have been obtained as follows:

(*a*) The abundance of the various species, as found by direct observation of living cells (see p. 198), was noted by the symbols a. (abundant), f. (frequent), o. (occasional), r. (rare) and v.r. (very rare). These symbols were given the numerical values of 16 (a.), 8 (f.), 4 (o.), 2 (r.), 1 (v.r.), as each represented roughly double the abundance of the one below. The sum obtained by adding together the values for all the species observed alive on any one soil is called the *productivity number* and is a rough estimate of the richness of the flora.

(*b*) The diversity of the flora is shown by listing the presence or absence of more than six species seen alive.

(*c*) Readily available phosphate is expressed as the percentage of P_2O_5 present (see p. 198). The interpretation of chemical estimations of the inorganic constituents of the soil relative to the needs of higher plants is often of considerable complexity (Davies, 1940). Estimations of 'available' or 'active' forms (usually those fractions soluble in weak solutions of acetic or citric acids) are commonly used for agricultural advisory purposes (Davies, 1940, p. 4 et seq.). It is not known how far such methods are applicable to the needs of soil algae, but, until suitable methods have been devised, these are the only ones available. Using $0.5 N$ acetic acid as the extracting liquid, it has been suggested that a phosphate content below 0.012% P_2O_5 is to be considered as slightly low to low, $0.012-0.015 \%$ as fairly satisfactory and larger amounts as satisfactory, where crops are concerned and the organic content of the soil is less than 15% (Davies, 1940). With increasing organic content these criteria must be raised approximately 0.001% for every 1% increase of organic content from 15 to 30%. With 40% or more organic matter these analyses are not reliable (Davies, 1940, p. 7; Stewart, A. B., private communication). A somewhat similar state of affairs appears applicable to soil diatoms. Allowance must be made for the fact that I have passed the soil through a 1 mm. mesh sieve, while one of 2 mm. mesh is commonly used. This will result in somewhat higher phosphate contents, since the finer sieve will remove more of the inert particles (the reverse is often the case with the carbonate content).

I have reversed the above procedure, and instead of raising the percentage of P_2O_5 considered as satisfactory with increasing organic content, I have reduced the estimated phosphate content by 0.001% for every 1% increase in organic content between 15 and 30%.

Similar criteria have been applied to the readily available potash (not shown in Fig. 1). Using these criteria and including the pH, presence or absence of nitrates (see p. 198)

and calcium carbonate, the soils may be divided into two groups, those giving a positive reaction for base-deficiency with the Comber-Misra test (p. 198), and those giving a negative reaction.

(i) *Productivity*

(a) *The base-deficient* soils, twenty-five in number and all more acid than pH 6·0. Nearly all contain less than 0·015% available phosphate, no nitrates and no calcium carbonate. With these features go generally a productivity number of under 20 (often under 10), and less than seven different species observed alive on the soils. Five soils (S19, 12, 49, 58, 18) contained over 0·015% available phosphate with a productivity number of under 20, but only S12 and 49 contained nitrates. Four soils (S7, 12, 49, 6) contained over 0·015% available phosphate and nitrates, and, of these, two (S7, 6) had a productivity number of over 20. Thus only S12 and 49 possessed a productivity number of under 20, despite the presence of over 0·015% available phosphate and nitrates, and S12 was the only base-deficient soil showing over six species alive on direct observation.

(b) The thirty-three soils which were not base-deficient (and all more alkaline than pH 5·8) generally contained over 0·015% available phosphate with nitrates and calcium carbonate present. With these chemical conditions there usually went a productivity number of over 20 (over 40 in 27% of the soils), and more than six species seen alive by direct observation. Four soils (S41, 36, 42, 43) contained over 0·015% available phosphate and a productivity number of under 20, but S41 and 36 lacked nitrates. On three soils (S54, 42, 43) there were less than six species observed alive, despite the presence of nitrates and over 0·015% available phosphate, and S16 had six present under these conditions. S42, 43 both had a productivity number of under 20, while S54 had recently been treated with a compound artificial fertilizer and was exceptionally rich in nitrates, available phosphates (0·198%) and potash. The only three species present (*Hantzschia amphioxus, Navicula pseudatomus, N. mutica*) occurred in vast numbers.

There was no clear correlation between available potash and productivity, though the majority of soils poor in diatoms were also poor in potash.

Thus, of fifty-eight soils, only four possessed a diatom productivity number of under 20 in the presence of nitrates and over 0·015% available phosphates. Two of these also showed less than six living species on direct observation, together with S54, which may well have contained excessive quantities of nutrients (see above and p. 207). Conversely, no soil containing both less than 0·015% available phosphate and giving a negative reaction for nitrates gave a diatom productivity number of over 20. In the case of S42, 43, these samples were collected in February, which would appear (p. 208) to be the least favourable period for growth; they were also rich in calcium carbonate (over 27%) which may have led to iron deficiency, and S43 was very poor in potash. Some exceptions may be expected in such a rough survey and substances other than nitrates and phosphates may act as limiting factors at times. It would appear that, using the present methods of analysis, nitrate and phosphate contents must be above certain limits to permit active growth of soil diatoms, their absence or poverty often being combined with deficiency in bases.* Highly acid soils may also be toxic, though

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* Chlorophycean productivity shows a different relationship to nutrients, as will be shown in a later paper.

Fig. 1. Diatom productivity and number of species in relation to chemical factors. For methods of compilation see p. 202. +, present; −, absent.

none here were rich enough to separate such an effect from poverty of nutrients. There is also the factor that, with high acidity, bacterial activity tends to be lowered and replaced by fungal action.

(ii) *Distribution of the species* (Table 1 illustrates this section)

While no clear correlation is to be found between the occurrence and abundance of the separate species and the separate nitrate, phosphate or potash contents of the soil, there is a relationship with base-deficiency, *p*H and calcium carbonate content. When making comparisons with the general richness of the soils, allowance must be made for the frequent poverty in nutrients of base-deficient soils.

Table 1. *Distribution of species relative to base-deficiency and *p*H*

(For explanation see below)

Alga	Percentage of total occurrences		*p*H range
	On base-deficient soils	On non-deficient soils	
Mainly on the more calcareous soils:			
Amphora montana	0	100	6·9–8·2
Navicula cincta var. Heufleri	0	100	6·9–7·4
N. cryptocephala f. terrestris	0	100	6·6–8·0 (6·0 v.r.)
N. minima	0	100	6·2–7·2
N. Muriella	0	100	6·4–7·5 (5·9 r.)
Nitzschia terricola	0	100	6·4–7·5
N. Tryblionella var. debilis	0	100	7·0–7·2
Surirella ovata	0	100	5·9–8·3
Nitzschia communis var. hyalina	4	96	5·9–8·2 (5·3 v.r.)
N. palea	5	95	5·9–7·4
Navicula mutica	6	94	6·0–8·3 (5·3 v.r.)
N. seminulum	6	94	6·0–7·3 (5·5 r.)
N. tenelloides	9	91	5·9–8·0 (4·6, 5·6 r.)
N. terrestris	13	87	6·4–8·0
Hantzschia amphioxus	18	82	5·1–8·2
Mainly on neutral to acid soils:			
Navicula contenta	24	76	3·9–8·3
Stauroneis montana	27	73	5·3–6·9
Pinnularia intermedia	32	68	4·8–8·0
P. microstauron	33	67	4·6–6·6 (6·9, 8·0 v.r.)
Navicula pseudotomus	42	58	4·4–8·3
Pinnularia subcapitata	47	53	4·5–6·4 (8·0 v.r.)
P. borealis	55	45	4·4–6·0 (7·4 v.r.)
Exclusively on acid soils:			
Caloneis fasciata	0	100	3·9–5·2
Pinnularia silvatica	0	100	4·5–5·2

In Table 1 the percentage of occurrences of the various species is based on frustules seen in the permanent mounts (of over 2 per coverslip), living cells in cultures and on enriched samples, as well as those seen alive by direct observation. Where the *p*H range is concerned, only specimens seen alive by direct observation are included. Where the species were present on one or two soils outside the main range of *p*H, these occurrences are placed in brackets, the *p*H being noted first and the frequency symbol second.

The frequency symbols, given in brackets after each species mentioned below, refer to the greatest abundance in which it occurred in any soil in the category concerned.

A. *Base-deficient soils*. On very acid (*p*H 3·7–4·7) soils, poor in available phosphates and lacking nitrates, only *Caloneis fasciata* (f., mainly moorlands) and *Pinnularia silvatica*

(f., confined to woodlands) occurred in quantity. Sometimes *P. borealis* (v.r.) and *Navicula pseudatomus* (o.) were present.

On soils of *p*H 4·7–5·9 containing over 0·015 % available phosphate, usually containing nitrates but lacking in carbonates, *Pinnularia subcapitata* (o.), *P. borealis* (o.), *P. microstauron* (a.), *P. intermedia* (o.) and *Navicula pseudatomus* (o.) were the main species present. The soils of this *p*H group, poor in nutrients, possessed too sparse a flora to give any indications of characteristic species, if such exist.

B. *Soils not base-deficient.* Such soils, containing calcium carbonate but lacking nitrates and poor in available phosphates, were very poor in diatoms, the usual species being *Hantzschia amphioxus* (o.), *Navicula mutica* (r.) and *N. pseudatomus* (v.r.).

On soils of *p*H 5·9–7·0 not poor in available phosphates, containing nitrates and less than 0·3 % CaCO₃ (usually only a trace), the characteristic species were: *Navicula pseudatomus* (a.), *N. Muriella* (v.r.), *N. mutica* (f., once), *N. seminulum* (a.), *N. tenelloides* (f.), *Pinnularia microstauron* (a.), *P. intermedia* (f.), *Hantzschia amphioxus* (f.), *Nitzschia palea* (f.), *Stauroneis montana* (f.), *Surirella ovata* (v.r.) and, from *p*H 6·4 onwards, *Nitzschia terricola* (f.).

Finally, on soils of *p*H 7·0–8·3, containing nitrates, not lacking in available phosphates and from 0·1 to 38 % CaCO₃ (usually over 1 %), the following species were characteristic: *Amphora montana* (f.), *Navicula pseudatomus* (a.), *N. mutica* (a.), *N. Fritschii* (f.), *N. cryptocephala* f. *terrestris* (f.), *N. tenelloides* (r.), *N. cincta* var. *Heufleri* (f.), *Hantzschia amphioxus* (f.), *Nitzschia terricola* (f.), *N. communis* var. *hyalina* (a.), *N. Tryblionella* var. *debilis* (f.).

The calcicole species, therefore, appear to be those of the last group less *Navicula pseudatomus* which occurred in abundance from *p*H 4·8 to 8·0. The only definitely calcifuge species are *Caloneis fasciata* and *Pinnularia silvatica*, though *P. microstauron*, *P. subcapitata*, *P. intermedia*, *P. borealis* and *Stauroneis montana* seem to be intolerant of more than small amounts of CaCO₃.

<center>(2) *Discussion in relation to previous investigations*</center>

(i) *p*H

My results support the views of Petersen (1935, p. 116) and John (1942) that diatoms are poorly represented in acid soils, though it is probably more precise to say base-deficient rather than acid, and the usual poverty of such soils in nutrients must be borne in mind. Nevertheless, even the base-deficient soils rich in diatoms showed a restricted number of species.

Petersen considers that the poverty of the flora is not exclusively due to the acidity of the soil, since, in certain acid high-moors, species of *Pinnularia* and *Eunotia* occur in quantity. He is, however, here referring to more or less purely aquatic species and not to eu-terrestrial forms, which are poorly represented in his own soil collections from acid habitats (1915, 1932*a*, 1935). Stokes (1940) has brought forward evidence that liming has a beneficial influence on the development of surface soil algae, though he does not particularize the groups concerned.

(ii) *Nitrogen*

Petersen (1928, 1935) suggests that nitrogen content is one of the most important conditions, though he has not made any analyses. In the case of Phanerogams there is

considerable difficulty in assessing the value to be placed on estimations of nitrogenous compounds. He specially mentions *Navicula pseudatomus* (*N. atomus* in his and John's account), but John (1942, p. 334) found in a series of five soils from a grass heath that the only one lacking *N. pseudatomus* was the most acid (*p*H 3·7), and this contained the highest nitrogen content. She considers, therefore, that $CaCO_3$ or *p*H have a stronger influence. In the present series of soils *N. pseudatomus* occurred in abundance over a *p*H range of 4·8–8·0, so that John's view can hardly be correct. Though it is not stated, it is probable, from the *p*H of John's acid soil, that she is referring to total nitrogen content. At that *p*H in an uncultivated soil available nitrogen compounds (e.g. nitrates) may well be absent (cf. Pearsall's results (1938); nitrates were almost constantly absent below *p*H 3·8). One of my samples giving a negative reaction for nitrates (S 58) did contain a large number of *N. pseudatomus*. However, it must be remembered that nitrates are quickly leached out of soil, an effect which is likely to be particularly severe in the surface layers, and the absence at any one particular time may be only of a temporary nature. It may be, therefore, that Petersen's view is correct. On the other hand, it must be remembered that other diatoms show a similar relationship to the presence of nitrates. This is because the soils deficient in nitrates were also deficient in diatoms.

It is quite clear that here, as in Denmark and Iceland, it is the well-cultivated garden and allotment soils that usually have the richest diatom flora. Gistl (1933) has brought forward similar evidence for soil algae generally, but many of the species which arose in his cultures are almost certainly not true soil algae. Such soils may be expected to be not only rich in nitrogenous matter but also in potassium, phosphate phosphorus and other nutrients.

(iii) *Phosphates*

Chu (1942, 1943) has shown for several planktonic algae that, though the lower concentrations found in fresh water are often below the lower limit for optimum growth, the highest concentrations are always lower than the upper limits for optimum growth in cultures. Further, so long as both nitrogen and phosphorus concentration are within the optimum range for growth, no change in their ratio markedly affects the growth of the algae concerned. While the largest growths were obtained on soils with over 0·025 % available phosphate, it does not appear that over this amount, at the most, increasing amounts yield correspondingly richer floras. Nitrates were almost always present in such soils. Where heavy doses of artificial manures, especially of single salts, are applied to the surface of the soil, toxic concentrations may be reached. In two cases this appeared to have occurred, but the effect was not of reduced total productivity but of restricted flora. In each case (S 54, SF) a heavy dose of a compound fertilizer had recently been applied. S 54 showed 0·198 % available phosphate, over 0·025 % available potash and a powerful reaction for nitrates even when the extract for testing was diluted more than three times. In each case the same three species occurred in vast numbers (*Hantzschia amphioxus, Navicula mutica, N. pseudatomus*) to the exclusion of all others.

(3) *Seasonal variation and micro-stratification*

These were only studied in one soil (see Fritsch, 1936; John, 1942, p. 342 et seq.). It may be noted as regards micro-stratification, however, that whereas only the

surface was added to the agar cultures, complete slices of soil to approximately 2 cm. thick were used for the enriched samples. The floras arising from these two sets of cultures did not differ materially. John (1942) studied successive 1 cm. layers of soil down to a depth of 4 cm. by means of cultures only. For the soils studied, she found that diatoms, with the exception of *Hantzschia amphioxus*, were commoner below than on the actual surface. This is completely different from what I have found from direct observation. In a number of soils rich in diatoms, though not studying micro-stratification, I did remove the surface to about 1 mm. deep, and in every case the number of diatoms was very much reduced; in some cases it was the difference between a rich and a very poor flora. All my examinations point to diatoms being surface forms, and it is especially noticeable that, in enriched samples, they crowd on to the lower surfaces of the coverslips (see p. 198). In the case of the one soil studied in some detail, there were no species more common below than on top of the soil, and the same striking diminution in total number was noticed.

On the other hand, John may well have examined drier soils than mine, since I have not collected during periods of long drought (see p. 197) apart from this soil. Equally some of her soils may have been of more open texture. Under prolonged drought the soil diatoms might tend to move below the surface to moister regions, while an open texture may also favour micro-stratification. There was no evidence of any such movements in enriched samples, which were allowed to become air-dry.

Seasonal variations, though not sharp, did occur with maxima in spring and early summer (Table 2 illustrates the flora of this soil) as is general with soil algae (cf. Petersen, 1935, pp. 122–3) and again in autumn. The first maximum may be longer or shorter according to the rainfall. This was a garden soil so situated that it only received the afternoon or evening sun from early spring to late autumn and none at all in winter. In consequence it remained moist longer than the majority of soils, but summer droughts reduced the number of diatoms considerably (e.g. Table 2, compare June with May and July 1939). The least growth was usually seen in February, a period of apparently poor growth in other soils (e.g. soils 42 and 43, Table 1). The species did not show any seasonal succession.

This soil was not manured and had not received any special treatment at least 3 years prior to this investigation. It was kept free from weeds. Under natural conditions such a soil would be completely covered with vegetation in a relatively short time, and though there may be little regular seasonal variation in productivity on such a cultivated soil, there are clear suggestions of it on woodland and other soils which are more or less bare for only a part of the year. There, general observations have shown that little or no growth of algae is macroscopically visible from midsummer to early spring when the surface is covered by higher plants and their remains. From early spring to summer, the absence of leaves on the trees and decomposition of the plant remains result in the most favourable light conditions. These are combined with higher (but not too high) temperatures and, usually, plentiful water supplies. The growth of algae is then often great enough to be visible to the naked eye.

Table 2. *Periodicity on a garden soil*

Month	1939 iv	v	vi	vii	ix	xi	1940 vi	1941 ii	vi	vii	1942 ix	x	xi	xii	1943 i	ii	iii	iv	v	vi	vii	viii	ix	x	xii	1944 i
pH	6·3	6·4	6·4	6·4	6·6	6·6	6·2	6·8	6·8	6·6	5·4	5·7	5·3	5·2	5·5	6·8	6·1	7·1	6·2	6·2	6·2	6·6	6·4	6·3	6·4	6·3
Diatoms:																										
Stauroneis montana	v.r.	r.	—	r.	v.r.	v.r.	v.r.	—	—	—	o.	f.	v.r.	r.	r.	v.r.	r.	v.r.	v.r.	r.	v.r.	v.r.	o.	o.	r.	—
Navicula pseudatomus	a.^{2}(d)	a.^{2}	v.r.^{3}	o.^{3}	f.^{4}(d)	v.r.^{3}	—	—	r.^{2}	o.^{4}(d)	o.^{2}(d)	r.^{4}(d)	r.^{4}(d)	o.^{4}(d)	—	v.r.^{4}(d)	f.^{3}(d)	a.^{4}(d)	a.^{3}(d)	o.^{3}(d)	f.^{4}(d)	f.^{4}(d)	o.^{4}(d)	r.^{4}	o.^{4}	r.^{4}
N. seminulum	a.^{3}	a.^{2}	v.r.^{3}	o.^{4}	f.^{4}	v.r.^{3}	f.^{3}	v.r.^{2}	f.	o.^{4}	o.^{3}	r.^{4}	r.^{4}	o.^{4}	v.r.^{2}	v.r.^{4}	f.^{3}	a.^{4}	a.^{3}	o.^{3}	f.^{4}	f.^{4}	o.^{4}(d)	r.^{4}	o.^{4}(d)	r.^{4}(d)
N. minima	a.^{3}	o.	v.r.^{3}	o.^{4}	f.^{4}	—	f.^{2}	v.r.^{2}	r.^{2}	o.^{4}	—	r.^{4}(d)	r.^{4}	o.^{4}	v.r.^{2}	v.r.^{4}	f.^{3}	a.^{4}	a.^{3}	o.^{3}	f.^{4}	f.^{4}	o.^{4}(d)	r.^{4}	o.^{4}	r.^{4}
N. muralis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	v.r.^{4}	—	a.^{4}	—	—	—	f.^{4}	o.^{4}(d)	r.^{4}	o.^{4}	r.^{4}
f. agrestis	—	v.r.	—	o.	o.	v.r.	r.	v.r.	v.r.	v.r.	v.r.	v.r.	v.r.	v.r.	—	o.	v.r.	v.r.	v.r.	—	—	v.r.	v.r.	—	v.r.	v.r.
N. cincta var. Heufleri	—	—	—	—	—	—	—	—	—	—	—	—	v.r.	—	—	—	r.	v.r.	v.r.	—	—	r.	f.	—	—	—
Pinnularia intermedia	—	—	—	—	—	—	—	—	a.	f.	o.	a.	f.	f.	o.	r.	f.	f.	f.	o.	o.	f.	f.	a.	a.	a.
P. microstauron	f.	a.	r.	o.	f.	r.	a.	r.	r.	r.	r.	r.	f.	v.r.	r.	r.	r.	f.	r.	r.	v.r.	—	o.	r.	v.r.	r.
P. viridis	r.	o.	v.r.	r.	r.	r.	r.	v.r.	—	—	—	—	r.	v.r.	v.r.	v.r.	r.	v.r.	v.r.	v.r.	v.r.	v.r.	—	v.r.	—	o.
P. subcapitata	v.r.	v.r.	—	o.	r.	r.	—	—	v.r.	—	r.	v.r.	r.	v.r.	v.r.	v.r.	v.r.	o.	—	v.r.	v.r.	—	r.	v.r.	—	v.r.
Hantzschia amphioxus	v.r.	—	—	—	—	—	—	v.r.	f.	v.r.	r.	v.r.	—	v.r.	v.r.	—	v.r.	r.	—	—	—	v.r.	v.r.	—	—	—
Nitzschia communis var. hyalina	f.	v.r.	v.r.	o.	a.	v.r.	o.	v.r.	r.	v.r.	f.	f.	o.	r.	v.r.	v.r.	r.	o.	v.r.	o.	a.	o.	f.	f.	o.	r.
N. palea	—	v.r.	v.r.	—	—	v.r.	—	v.r.	r.	—	v.r.	v.r.	—	—	v.r.	v.r.	r.	v.r.	—	v.r.	—	—	v.r.	v.r.	—	v.r.
Surirella ovata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—	—	—	—	—
Other diatoms	6	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Productivity no.	37	47	6	25	41	11	34	3	38	11	35	39	20	19	13	12	30	42	30	20	31	26	32	36	28	29

For 'productivity number' see p. 202. Where the frequencies of two or more species could not be completely separated by direct observation in the four *Navicula* spp. which are bracketed, the figure 2, 3 or 4 is placed after the symbols, according to the number present, and a (d) after the symbols. The pH 7·1 for 1943·iv was caused by the temporary presence of plaster dust on the surface.

E. THE SIZE FACTOR

(i) *The relative size of soil and aquatic specimens*

Petersen (1915, p. 359), Fritsch (1922 b, p. 222) and Bristol (1920, pp. 40–1) have pointed out for soils, and Beger (1927, p. 391) for moss tufts, that the diatom flora consists almost exclusively of small species or small forms of larger species. Particular attention has been paid to *Hantzschia amphioxus* (Table 3; see also Petersen, 1935, p. 149), the largest soil diatom observed by these workers, which reached 80 μ long in Danish soils, 60 μ in British soils, rarely 100 μ in moss tufts (Beger, 1927) and 50 μ in Gistl's (1931–2) cultures.

That the soil flora consists mainly of small species is self-evident, only eleven of the diatoms here recorded reaching over 50 μ long even when growing in aquatic habitats, and only three of these attained this length in soils.

That the largest species occur only as small forms in soil is more difficult to prove. The largest cells are the immediate descendants of the auxospores and, as cell division continues, the percentage of smaller cells present becomes larger and larger (Fritsch, 1935, p. 617). Further, auxospore formation is comparatively rare in nature, even a year or more passing between one phase and the next (see Fritsch, 1935, p. 617, as regards planktonic diatoms), the process being dependent, in pennate diatoms, on the cells being between certain size limits at a time when the environmental conditions are favourable (Geitler, 1932). Hence, in any one relatively small soil sample, such as was taken in the present investigation, the largest cells may not be present. The environmental conditions favourable for auxospore formation, once the necessary size limits are reached, which appear also to be those favourable for the most active vegetative growth (Geitler, 1932: *Navicula seminulum* and *Gomphonema parvulum*), may only occasionally occur in soils, and then, owing to the relatively rapid changes in the moisture content of the soil surface, only for short periods. The restocking of many soils, as the diatoms reach a minimal size and die out, may largely take place from specially favourable centres. I have not observed any auxospore formation in nature, though the changes in size observed in some cultures suggested strongly that it had occurred in them.

Soil conditions may favour the smaller cells (see pp. 215–19). The size of the cells able to form auxospores seems to be commonly above half-way between the maximum and the minimum (see figures for *Navicula seminulum*, *Gomphonema parvulum*, *Achnanthes lanceolata*, etc., in Geitler, 1932), and hence, though auxospore formation may be inhibited, the cells can go on dividing for a considerable time. A very large number of descendants are potentially possible from a single auxospore (Fritsch, 1935, p. 617).

Lastly, there does not seem to be any information as to whether the size of the frustules arising from the auxospores can be altered by changes in the environment after auxospore formation has been initiated. Their normal size seems to vary but little from the maximum size possible (Geitler, 1932).

Practically nothing is known as to how diatoms resist drought, since, with a few possible exceptions, they do not produce any known resting stages (see Fritsch, 1935, p. 638); Petit's (1877) account is not altogether clear and does not appear to have been corroborated).

Nevertheless, despite these arguments, from the examination of more than 1300 preparations from over sixty soils and cultures, it does appear that the soil forms of the

larger species are smaller than the corresponding aquatic forms (see Table 3), while in the case of the smaller species which are neither entirely nor predominantly terrestrial, the differences in maximum size are less marked or absent. It will be seen in Table 3 and in the taxonomic section that the minimum size recorded is, in almost all cases, lower than previously recorded for aquatic or semi-aquatic habitats, even in species whose maximum size is as large as or larger than previously recorded (e.g. *Navicula contenta, Caloneis fasciata*). This may, however, be due to the large numbers of cells examined (compare, in Table 3, Geitler's (1932), measurements, based on extensive cultures, of *N. seminulum* with those of Hustedt (1930)).

Good examples of reduced size are provided by *Pinnularia microstauron, P. viridis* and *Nitzschia palea* (Table 3). The first and last were often frequent and sometimes abundant on the soils and in enriched samples, and all three were examined at intervals for over 5 years on the same soil, so that it seems almost certain that the maximum size has been observed. *Hantzschia amphioxus* reached a larger size than recorded by Petersen (1915) or Bristol (1920) in a number of soils and cultures. Specimens over 100 μ long occurred on four soils. This was markedly below the maximum recorded (var. *maior* Grun.) for aquatic habitats, though var. *maior* may be a true variety rather than a collection of maximum-sized individuals. Bristol (1920) only found a maximum length of 60 μ, though she grew cultures of it from forty-one soils. My records show that this length is frequently exceeded in nature, and it seems clear that auxospore formation never occurred in her cultures. This was probably due in part to the solution being too concentrated (cf. Chu's (1942) solutions for planktonic diatoms and Bristol (1920, p. 390)) and to the necessity of regular subculturing (Geitler, 1932). Other species occurring in several soils and cultures which were markedly smaller than recorded for aquatic habitats included *Pinnularia borealis* (never present in quantity; cf. Beger's specimens from moss tufts (1927)), *P. subcapitata* and *Surirella ovata*.

Clearly this question can only be solved by growing clone cultures under varied conditions and by further direct observation on soils, but it is, at least, a remarkable coincidence that all the workers on soil diatoms have noticed this size difference.

(ii) Size and form

Geitler (1932, p. 175 et seq.) has shown for various pennate diatoms that the smaller cells are not geometrically proportional to the larger ones from which they arise, but that certain alterations in form occur with decrease in size. These, besides their intrinsic interest, are of importance in studying the taxonomy ((iii), p. 214) and ecology ((iv), p. 215) of soil diatoms. When not dealing with clone cultures, the possibility that differences observed are not changes in form with decrease in size but are due to the presence of two or more forms of varying size, must be borne in mind. The conclusions reached by Geitler on which observations were made here were as follows:

(*a*) The apical axis decreases in length not only absolutely but also relatively more than the transapical axis, and hence the smaller are relatively wider than the larger valves. This was of general occurrence (e.g. *Stauroneis montana* var. *elongata*, Fig. 3 DD–JJ; *Navicula seminulum*, Fig. 5 I–O; *N. minima*, Fig. 5 A–H) and especially well marked in the larger species (e.g. *Pinnularia viridis*, Fig. 12 K–N; *P. intermedia*, Fig. 12 A–J; *P. microstauron*, Fig. 11 A–E, P–R; *Surirella ovata*, Fig. 18 O–T, X–AA; *Nitzschia parvula* var. *terricola*, Fig. 14 A–I), and least well marked in the oval-elliptical species

Table 3. *Valve measurements (in μ) and number of striae, etc. in 10μ*

	Aquatic habitats			Terrestrial habitats		
	L.	Br.	Str.	L.	Br.	Str.
Frustulia vulgaris	50–70	10–13	24	34–42	8–9	28–31
Caloneis fasciata	20–30	4–5·5	25	10–30	4–7	25–30
Including						
Pinnularia fasciata (sensu Hustedt)	(1) 23–27	5–8	24–26	(2) 17–22	4–5	23–25
Navicula seminulum	11–16	4	18–20	4–18	2·5–5	20–30
	(3) 4–18	3–4·5	18–23			
N. minima (incl. var. *atomoides*)	8–17	2·5–4·5	26–30	4–15	2–4	28–35
N. mutica	10–40	7–12	15–20	6–30	4–8	18–27
				(4) 10–30	5–7·5	14–17
				(5) 9–?	4·5–?	20–25
N. contenta	7–15	2–3	App. 36	7–19	2–3	App. 35
				(4) 9–12	3–3·5	38
N. pseudatomus	4–8	2–4	App. 30	5–8	2–3	28–30
N. cryptocephala (incl. vars. *veneta* and *exilis*)	13–40	5–7	14–20	13–23	4–6	15–20
N. terrestris	20–45	6–10	13–16 centre to 22 apical	13–33	4–7	20–25 centre 25–30 apical
				(v) 15–37	4·5–8·5	18 centre to 25 apical
N. cincta (incl. var. *Heufleri*)	20–40	5–6	10–17	8–28	4–10	11–13
				(5) 12–?	4·5–?	10
Pinnularia molaris	33–50	5–8	15–20	23–43	5–6	14–20
P. microstauron	20–80	7–11	10–13	15–38	5–7	13–20
				(5) 15–17	4·5	App. 10
P. subcapitata	25–50	5–6	12–13	23–39	4–5	11–13
				(2) 22–?	4–?	
P. intermedia	18–42	6–8	8	12–35	4–5	9–12
				(4) 17–27	4·5–6	10–12
				(2) 13–33	4·5–7	8–12
P. borealis	28–110	8–18	4–6	22–46	5–8	5–6
				(6) 18·5–52		
				(4) 40–44	8·5	6
P. viridis (excl. var. *sudetica*)	30–170	8–30	6–9	22–94	8–13	8–12
Stauroneis anceps	25–130	6–18	20–30	26–34	7–8	26–27
Hantzschia amphioxus (incl. var. *maior*)	20–200	3–15	5–8 13–20	17–110	4–15	4–9 14–25
				(4) 30–60	6·5–7	7–10
				(5) ?–80		20
				(6) 20–30–100		
Nitzschia Tryblionella var. *debilis*	13–25	7–8	12–14 7–9	14–21	6–8	18–20 8–10
N. Hantzschiana	25–50	3–5	7–10 24	10–40	2–4	9–14 27–30
N. palea	20–65	2·5–5	10–15 35–40	16–34	3–5	12–15 30–36
				(4) 15–33	4	11–15
Surirella ovata	15–70	8–23	4–7 11–20	6–39	5–8	6–9 20–30

Valve measurements of species in both aquatic and terrestrial habitats. The former taken from Hustedt (1930) and the latter from the present survey unless otherwise stated, when the authority is given in brackets before the measurement concerned—viz. (1) Cleve (1894–5); (2) Petersen (1928); (3) Geitler (1932); (4) Bristol (1920); (5) Petersen (1915); (6) Beger (1927). Where carinal dots or ribs are present as well as striae (e.g. *Nitzschia*) the former are given above the latter.

(v) *Navicula terrestris*; here numerous authorities are concerned (for which see Part 2), and all aquatic records are grouped together and the terrestrial ones other than my own are prefixed by (v).

N. pseudatomus n.sp. is considered to be synonymous with *N. atomus* (Naeg.) Grun. of most authors, but not of Hustedt (1930); see Part 2 for taxonomy of this species. For abbreviations see p. 201.

(*Navicula muralis* f. *agrestis*, Fig. 8 A–H; *N. pseudatomus*, Fig. 6 K–W; *N. fossalis*, Fig. 7 H–K). Geitler (1932) has put forward the hypothesis that there is an inner relation between valve form and alteration in the course of division; that the more elongated the auxospore valve the relatively wider it becomes during the course of division.

In *Nitzschia Hantzschiana* (Fig. 16 B–J) the smaller valves were often absolutely wider than the larger even where there was no evidence that two separate races were concerned, since all gradations occurred in several cultures. A similar widening of the transapical axis was noted for *Diatoma vulgare* and for the smallest, often deformed, cells of *Eunotia formica* by Geitler (1932, p. 80, fig. 40; p. 96). It is not clear how such a change could come about in a cell with a rigid external wall.

(*b*) The length of the apical axis decreases not only absolutely but also relatively more than the width of the pervalvar axis. Hence, in girdle view, the smaller are relatively wider than the larger cells. This too (Table 4) is a general feature, but often the decrease in length of the pervalvar axis is too small to measure accurately.

Table 4. *Variations in length of the three axes of seven soil diatoms. The length of the pervalvar axis of the heteropolar* Surirella ovata *is given as the mean of the maximum and minimum for the cell*

Diatom	Range of length in μ of axes		
	Apical	Transapical	Pervalvar
Stauroneis montana	8–16	2·5– 4	2·5– 4
Navicula seminulum	4–18	2·5– 5	1·5– 2·5
N. cincta var. *Heufleri*	8–28	4–10	3– 5
N. mutica	6–30	4– 8	4– 5
Pinnularia intermedia	12–35	4– 5	5– 6
P. viridis	22–94	6–13	8–15
Surirella ovata	6–39	5– 8	5– 6

(*c*) The outline of the valve is less complex and more evenly rounded in the smaller than in the larger cells. This is well seen in the variable *Navicula mutica* (Fig. 6 A–H), the triundulate and strongly capitate or rostrate form of which is only seen in the larger cells; in *Navicula ignota* and var. *palustris* (Fig. 4 O–V, Y–CC), *Stauroneis truncata* (Fig. 2 U–AA), *S. montana* (Fig. 3 K–X); *Navicula Fritschii* (Fig. 7 A–G); *Nitzschia parvula* var. *terricola* (Fig. 14 A–I) and *Surirella ovata* (Fig. 18 O–T, X–AA).

(*d*) The density of the valve markings remains, within narrow limits, constant for a given diatom, any increase in density with decrease in cell size being small compared to the decrease in the length of the valve. While the density of the striae does not increase nearly so much as the apical axis decreases, the increase with decreasing cell size is often appreciable (see also (iii) below).

(*e*) An additional feature, not recorded by Geitler, seen in some soil diatoms, is the alteration in the orientation of the striae. In *Pinnularia viridis* the more central radial striae of the larger valves (Fig. 12 M, N) become parallel in the smaller valves (Fig. 12 K, L), and, to a less extent, the more apical striae become less markedly convergent. In *P. intermedia* the strongly radial central striae also become parallel (Fig. 12 H, I) or even convergent (Fig. 12 J; cf. Petersen (1928, p. 405, fig. 24*a–f*) and *P. saxicola*, Fig. 10 G–I) in the smaller cells. In *Navicula cincta* var. *Heufleri* it is the apical striae

whose orientation alters from convergent (Fig. 9 A, B) to parallel or radial (Fig. 9 D–F) with decrease in cell size. In *Caloneis fasciata* the weakly convergent apical striae (Fig. 2 L, M) become parallel (Fig. 2 T).

This change in orientation has only been observed in species whose larger valves have differently oriented striae centrally and apically.

(iii) *Size and taxonomy*

Geitler (1932, p. 186) has pointed out that the results of his observations on size and form make it clear that some described varieties and forms are merely stages in the growth cycle of one and the same diatom. My own observations agree with his. Size of cell, shape of valve, orientation and density of striae may be altered considerably during the growth cycle (see (ii) above), so that if only the extremes in size are observed, they would be considered as separate forms, varieties, or even species. The first- and last-mentioned features particularly tend to alter together. Hence it has been necessary in many cases to figure a series of cells of diverse sizes.

A further complication, in the case of soil diatoms, is that, though the size of the larger individuals does come within the range recorded for that species in aquatic habitats, it does not reach the maximum (barely half-way in some species, Table 3). Since, in the range over which they overlap, the soil and aquatic forms are nearly always indistinguishable (cf. Beger (1927) re *Pinnularia borealis*), and since it is not absolutely certain that in all cases the maximum possible size of the soil forms has been observed, there are no grounds for separating them from the aquatic ones on the basis of size alone. They may well be separate varieties, but further work is needed to prove this.

(*a*) *The striae*. Geitler (1932) has referred to the fact that the density of the striae has long been used as a characteristic, and that, within narrow limits, it is constant. These limits are, however, wide enough to necessitate caution in using density as a distinguishing feature. This is especially the case in the smallest cells. Thus, the cells of *Navicula seminulum* normally have between 20 and 25 striae in 10 μ, but the smallest specimens may have 30 striae. The estimation of the density is especially difficult in the minute cells, for a length of 10 μ is rarely available along which to measure the density, and measurements over lesser lengths often show appreciable variations over different parts of the valve. There is, further, an inherent error due to the fact that the length measured starts with a stria which itself may be of appreciable width. By measuring the striae along less than 10 μ and multiplying by the necessary factor any error is multiplied equally. Wherever possible, the number of striae over at least 20 μ length should be counted to obtain an average density for 10 μ.

With the increase in density there often, but not always (e.g. *Navicula cincta* var. *Heufleri*), goes also a decrease in width and clarity of the striae (e.g. *Navicula seminulum*, Fig. 5 I, P, X, Y, AA, CC, M–O, TT–VV; *Hantzschia amphioxus*, Fig. 13 A–F) which make the identification of some specimens very difficult.

The density and width of the markings are, however, of considerable value in separating some soil diatoms, if not so trustworthy in comparing soil and aquatic specimens of the same species (Table 3). Thus the larger linear valves of *Navicula seminulum* and *N. minima* can best be distinguished by the differences in the density and width of the striae (Fig. 5 A, I).

Differences in the orientation of the striae are generally considered to be of specific importance, but the gradual changes seen in some soil diatoms (see (ii) (*e*), above) show that this is not always the case, provided that these alterations in orientation are connected with the decreasing size of the cells in the course of subdivision.

(*b*) *The shape of the valve* is an important characteristic, but Geitler's (1932) observations and the present investigation show that this too must be treated with caution. Thus, the shortly elliptical to oval cells (Fig. 9 D–F) of Petersen's forma *curta* of *Navicula cincta* var. *Heufleri* are simply the smallest valves in the growth series of the variety. Similar size relationships hold for some of the rostrate and capitate (Fig. 3 K–X) valves of *Stauroneis montana*; the shortly ovoid (Fig. 18 S, T, AA) and elongated ovoid to linear-ovoid (Fig. 18 L–Q) valves of *Surirella ovata*; the rostrate constricted (Fig. 2 U, V) and linear cuneate (Fig. 2 Z, AA) valves of *Stauroneis truncata* and the linear (Fig. 10 V) and linear capitate (Fig. 10 T, U) valves of *Pinnularia subcapitata* and *Navicula ignota* var. *palustris* (Fig. 4, Y, Z, CC).

Here again the alteration in form is combined with alteration in size, but, as Geitler (1932) has pointed out, the fact that, of two types observed, the one is larger and has a more complex outline, while the other is smaller and has a less complex outline, may lead one to suspect that the smaller simply consists of the later products of the division of the larger, but there always remains the possibility that these are two separate diatoms. Thus, the various forms of *Stauroneis Muriella* (Fig. 4 A–I) appear to be distinct. Only clone cultures can decide which is correct, but if all gradations between the two types are seen and the 'simpler' of the two is consistently composed of the smaller cells, then it is almost certain that the two types are the products of the division of one and the same diatom.

This simplification of form with decreasing size sometimes leads to considerable difficulties in separating the smallest cells of different species (e.g. *Pinnularia microstauron* and *P. molaris*; *Stauroneis Borrichii* and *S. truncata*, Part 2). Further, features used to distinguish the larger cells of two clearly separate species may not be suitable for distinguishing the smaller. In the large linear cells of *Navicula seminulum* and *N. minima* (Fig. 5 A, I) the distinguishing features lie in the density and fineness of the striae, but in the smallest cells either these features, often combined with differences in the curvature of the striae (Fig. 5 HH, NN) or the shape of the valve, together with a slight difference in the density of the striae, with or without differences in fineness (Fig. 5 G, H, O, TT, UU), may be the distinguishing features.

(iv) *Size in relation to habitat conditions*

(*a*) *Water*. The view put forward (Petersen, 1915, but not mentioned in 1935; Bristol, 1920) and, apparently, based on Hedlund (1913) that small forms resist drought better than large ones, is contrary to what would be expected. Maximov (1929) has pointed out, for higher plants, that reduction in cell size can often be correlated with increased resistance to various unfavourable conditions and that spores are generally small. He adds that the cause of this greater power of resistance of small cells is unknown. Against this view it may be pointed out that the small size of spores may equally be related to distribution, and the small size of the cells of a higher plant is not necessarily accompanied by small size of the whole plant. If the three axes of the cell decrease in length proportionately to one another, there will be an increasing ratio of surface to

volume, so that, other things being equal, the smaller the cell the more severe the effects of desiccation. However, though soil diatoms possess no pronounced processes, with decrease in size there does go a simplification in form (see above and Geitler, 1932), so that the relative increase in surface area with decreasing size is mitigated. Further, since the decrease in size is very largely a decrease in the length of the apical axis, the decrease in the length of the transapical axis being much less and that of the pervalvar axis even smaller or virtually absent, the smaller the cell the nearer the approximation to an oval or spherical shape.

Table 5. *Surface area and volume*

See below for explanation. S.A. = surface area in μ^2; v = volume (μ^3); Ap. axis, apical axis length of (μ); P.V. axis, average length (μ) of pervalvar axis for corresponding range of length of apical axis.

Diatom	S.A.	v	Ratio, S.A. : v
Pinnularia viridis	3682	9396	0·4 : 1
Ap. axis 25–50 ⎫	2536	6360	0·4 : 1
P.V. axis 10 ⎬	1118	2060	0·6 : 1
Ap. axis 51–90 ⎫	724	1190	0·6 : 1
P.V. axis 12 ⎭			
Pinnularia intermedia	645	730	0·9 : 1
P.V. axis 5	619	690	0·9 : 1
	545	630	0·9 : 1
	390	424	0·9 : 1
	192	213	0·9 : 1
Navicula cincta var. *Heufleri*	360	355	1 : 1
Ap. axis 12–15 ⎫	288	313	0·9 : 1
P.V. axis 3·5 ⎬	167	165	1 : 1
Ap. axis 16–21 ⎫	142	133	1·1 : 1
P.V. axis 4 ⎭	133	114	1·2 : 1
Navicula seminulum	173	107	1·6 : 1
Ap. axis 4– 8 ⎫	135	95	1·4 : 1
P.V. axis 1·5 ⎬	111	60	1·9 : 1
Ap. axis 9–14 ⎫	44	13	3·4 : 1
P.V. axis 2 ⎭	42	17	2·5 : 1
Navicula mutica	478	516	0·9 : 1
Ap. axis 15–34 ⎫	450	500	0·9 : 1
P.V. axis 5 ⎬	273	251	1·1 : 1
Ap. axis 5–14 ⎫	129	106	1·2 : 1
P.V. axis 4 ⎭	123	93	1·3 : 1
Stauroneis montana	192	137	1·4 : 1
Ap. axis 9–15 ⎫	173	119	1·4 : 1
P.V. axis 3 ⎭	113	69	1·6 : 1
	99	59	1·7 : 1
	74	45	1·6 : 1
Surirella ovata	347	376	0·9 : 1
Ap. axis 25–35 ⎫	311	314	1 : 1
P.V. axis 5·5 ⎬	167	159	1 : 1
Ap. axis 10–25 ⎫	111	86	1·3 : 1
P.V. axis 5 ⎭			

In estimating (Table 5) to what extent the relative increase in surface area due to decrease in size is counterbalanced by the decrease due to these changes in the shape of the cell, the curvature of the valve face may, generally, be ignored since it is relatively small, being rarely noticeable in girdle view. The results in Table 5 are based on various text-figures and measurements of the pervalvar axis (breadth in girdle view). Since the latter alters either a small amount or so little as not to be measurable accurately, an average value is taken for cells lying between certain lengths.* Where this average shows

* These values are given in the left-hand column of the table under the species concerned. They do not refer directly to the figures opposite them in the three right-hand columns.

measurable differences it is computed from the measurement of 100 cells taken at random. The surface area of the cell is computed as twice the area of the valve, as found by planimeter measurement, plus the length of the margin of the valve, using a map measurer, multiplied by the length of the pervalvar axis (i.e. twice the surface area of the valve plus the surface area of the girdle). To obtain accurate comparisons it would be necessary to follow the changes in dimensions of a number of clones. However, in the present case, the maximum possible changes in form with decrease in size have been taken and, hence, the relative decrease in surface area due to simplification in form with decrease in cell size can hardly be appreciably greater than here given. In the case of *Navicula mutica* it is unlikely that cells such as Fig. 6 D (=var. *nivalis* (Ehr.) Hust.) become as simple in outline as Fig. 6 H (=var. *Cohnii* (Hilse) Grun.), though a considerable degree of simplification in form does undoubtedly occur with the decrease in size.

It will be seen that, despite the alterations in form, the ratio of surface area, relative to volume, either increases or remains almost constant with decrease in size, and hence, generally, the smaller cells will have a relatively bigger surface from which evaporation may take place, than the larger ones.

The small size may well be of value in direct absorption of water and salts from the soil when it is wet enough to have particles covered by water films of appreciable thickness. Then, the smaller the cell, the greater the ease with which one side of it, at least, can be apposed to these films. While no special observations have been made on the cell contents, I can confirm Petersen's observation (1935, p. 104) that, under conditions of drought, quantities of oily matter occur in the cells, and like particles investigated by Piercy (1917), Fritsch (1922 a) and Fritsch & Haines (1923) may be connected with an increased resistance to drought. A similar appearance is, however, sometimes seen in old, though moist, cultures. It is possible that with decreasing size there goes an alteration in the consistency of the protoplasm, leading to a greater water-holding capacity. The conditions governing resistance to drought are probably akin to those causing resistance to cold (cf. Stiles, 1930). When investigating the movement of diatoms under increasingly dry conditions (see (iv) (d)), it was noticed that a large number of the cells died if the coverslip was allowed to become air-dry.

(b) *Nutrition*. It may well be possible for the soil diatoms to resist considerable desiccation (see above), and the absence of directly available water from the films surrounding the soil particles by absorbing moisture from the atmosphere but, for absorption of salts, free water must be available and hence, for the reason given above, small size is advantageous.

Bristol (1920, p. 41) quotes a suggestion that the small size and faint markings of soil diatoms (esp. *Navicula contenta*) are due to long starvation under unfavourable conditions. She points out that in her soils, as in mine, no change in form or size occurred under cultural conditions even when the cells were constantly submerged, while small size is general in all soils no matter what the conditions. The same argument can be used against Hustedt (1937–8, p. 462), who criticizes the view that *Hantzschia amphioxus* is characteristically a terrestrial or aerial species and considers its optimum development to be in more aquatic habitats. He says that the number of individuals should not be considered alone, since this may be related to lack of competition produced by the absence of less adaptable species. The average size reached in the habitat concerned

15

should be considered as well. On this view he disagrees with Petersen's (1935, p. 149) attempt to separate hydrophytic and eu-terrestrial varieties since, according to the ecological conditions, all intermediate forms can be obtained. The soil forms are the result of unfavourable conditions, and under better conditions such 'Kummerformen' can return to normal. However, Hustedt (1942) points out that the predominance of small *Navicula*'s with weakly silicified valves and faint markings is not due to lack of nutrients, because they occur in the company of other well-silicified diatoms (e.g. *Pinnularia*). Gistl (1931–2) has brought forward evidence to show that the sum of the chemical and physical conditions prevailing in a given soil is decisive, not only in controlling the algal association, but also the growth form of the separate species. He criticizes Bristol's (1920) view that the culture solution used is unimportant since, though the majority of the species may occur in all the solutions, their form may alter. Growing *Navicula cryptocephala* var. *veneta* and *Hantzschia amphioxus* in solutions containing various concentrations of either sodium sulphate or sodium thiocyanate, he found that the cells in the sulphate cultures were always larger than those in the thiocyanate ones, the relative differences being almost exactly the same in each species. Further, the size differed in different concentrations of sulphate. He states that the size of soil diatoms in a culture is dependent on the mixture and concentration of ions present and suggests that the faintness in the valve markings in soil diatoms may also be connected with nutrition. He criticizes Beger's (1927) view that the variously sized *Pinnularia borealis* found by him in the *Bryum argenteum* tufts were pure lines, and suggests that the varied salts present may have been responsible for the size differences. However, his own conclusions are open to criticism. Though I and other soil workers have examined soils of undoubtedly great diversity in available salts and have used varying cultural solutions, we have all found constantly small size of a similar order. Further, while the smallest cells in his cultures were from 70 to 90 % the length of the largest, in Geitler's (1932) cultures of various species the smallest were only 10–30 % the length of the largest. It seems very doubtful whether Gistl obtained the complete range of size, and, in the case of the *Navicula*, he states that he only observed auxospores in the 0·2 *M* sulphate cultures, while he makes no mention of any auxospores in the case of *Hantzschia* where the maximum size was only 49·5 μ. In the case of the thiocyanate cultures of the latter, growth was so poor that the 0·01 *M* solutions were the only ones where multiplication could be seen clearly and, instead of being able to base his measurements on 100 cells, he had to use 50. Under such conditions allowance must be made for the size of the original cells of the cultures and the decrease in size with subdivision in the absence of auxospore formation.

Gistl's experiments need repeating, using more than two species and clone cultures. It seems hardly possible that the small size of the soil diatoms, as compared with the aquatic ones belonging to the same species, is due to the salts present in the varied soil solutions, nor does this explain the predominance in the soil flora of species which are of similar small size both in aquatic and terrestrial habitats. It may well be that the soil forms are genetically different.

(c) *Movement*.* Petersen (1915) and Fritsch (1922*b*, p. 222) have pointed out that small size will enable the diatoms to move readily through the finer interstices of the soil. This will often enable them to return to the surface after being washed below it

* It has recently been reasserted (Merlin, 1944) that this is due to cilia, but this is not the view taken here.

and to move to more moist areas when the soil is drying out. There is also the possibility that soil diatoms are unable to move in the absence of free water, and hence close approximation to small soil particles will often be necessary to obtain a suitable surface for movement. To test this hypothesis, coverslips from young enriched samples (see p. 199), rich in diatoms, were mounted on slides in distilled water and roughly ringed by filter paper saturated with water. The coverslips were then allowed to dry, the diatoms being observed from time to time, but the surrounding filter paper was kept wet to ensure that the water under the coverslip should evaporate gradually. At the end of the experiment water was again run under the coverslip. The following diatoms were studied: *Amphora montana, Hantzschia amphioxus, Navicula cincta* var. *Heufleri, N. mutica, N. cryptocephala* f. *terrestris, N. pseudatomus, Nitzschia palea, N. terricola, N. communis* var. *hyalina, Pinnularia borealis.* In many cases small species of *Chlamydomonas* or chlorophycean zoospores, motile bacteria and small Protozoa were present, whose ability to move gave some indication of the free water still available. In all cases, once the visible water films had dried up, there was no movement, but on the addition of water at the end of the experiment, many of the cells began to move once more. Often there were small islands of soil under the coverslip which retained more water than was present under the remaining parts and, around these, diatoms could be seen moving when the remainder had ceased to do so. It is clear, therefore, that in the absence of a clear-water film around the soil particles, soil diatoms cannot move. In all cases movement ceased before the water films had disappeared from view.

(d) *Distribution.* The small size of soil diatoms will be of value in increasing the distance to which they may be carried as wind-borne dust. In this connexion it may be noted that, unlike many of the other soil algae, no resting stages are known for soil diatoms. Further, it is only in dry weather that any appreciable amount of soil dust is wind borne, and at this time the weight of a cell for any given volume is likely to be near or at its minimum, due to the evaporation of the more lightly bound water within the cells. The production of oleaginous matter in the cells during the periods of drought may well reduce their specific gravity and add to their buoyancy

(*Part 2—Taxonomy—to follow.*)

ON SEPAL PHYLLODY IN ROSES AND SOME RELATED PHENOMENA

EXPERIMENTAL DATA AND A QUANTITATIVE INTERPRETATION

By T. E. T. BOND

Tea Research Institute of Ceylon

(With 6 figures in the text)

Sepal phyllody is commonly regarded as a teratological manifestation and, as such, has rarely been the subject of sustained and quantitative study. An opportunity for this was afforded by the frequency of the condition in roses growing in Ceylon, where flowering is almost continuous throughout the year and the bushes come rapidly into bloom after pruning. The results obtained appeared of sufficient interest to warrant an account of them with some further applications to other related phenomena previously noted by the writer (1940, 1941).

DESCRIPTION

The roses, sixteen bushes in all, were growing on this Institute's estate near Talawakelle, C.P., at an elevation of 4500 ft. They were probably of Australian origin, although no records of their importation were available. The condition of phyllody (Fig. 1) consisted in the enlargement of the terminal, leafy appendage which is normally present at the apex of each sepal. This was accompanied, usually, by a tendency to produce leafy lateral segments, at any rate on the three outer sepals. However, even in the most marked instances there was no question of the complete replacement of the sepal by a perfect foliage leaf, as described by Masters (1869, fig. 129, etc.), Worsdell (1916) and, for an earlier Ceylon example, by Senaratna (1930). Nor, except very occasionally, were there any associated abnormalities: only one instance of a slight downward displacement of the first sepal was recorded, and a few examples of partial sepalody in one of the petals. The essential uniformity of the sepals is best seen by considering the calyx as a whole, whence it is found that the degree of leafiness follows the order of development, the innermost sepal being but little different from normal even when the outermost is highly modified. In most calyces, the phyllotaxy could be determined without difficulty; the interval was invariably two-fifths, although both right- and left-handed spirals occurred. In doubtful cases, the one-sided development of the third sepal, particularly with regard to the lateral segments where these were present, was a useful guide to the direction of phyllotaxy.

The degree of leafiness, even under the most favourable conditions (see below), depended to a considerable extent on the variety, of which four were distinguishable, as follows (seven bushes in variety 'A', and three in each of the others):

Var. 'A'—a typical H.T.; the flowers pale cream with a slight pink flush; young foliage red, buds very pointed, fruits smooth. The leafiness of the sepals was more

marked here than in any of the others, the largest recorded leafy lamina (Fig. 1A) extending to 5·5 × 3·0 cm. (See also Fig. 1 B.)

Var. '*B*'—very near 'A'; the flowers rather pinker and the leafy sepals usually somewhat longer in proportion to their breadth.
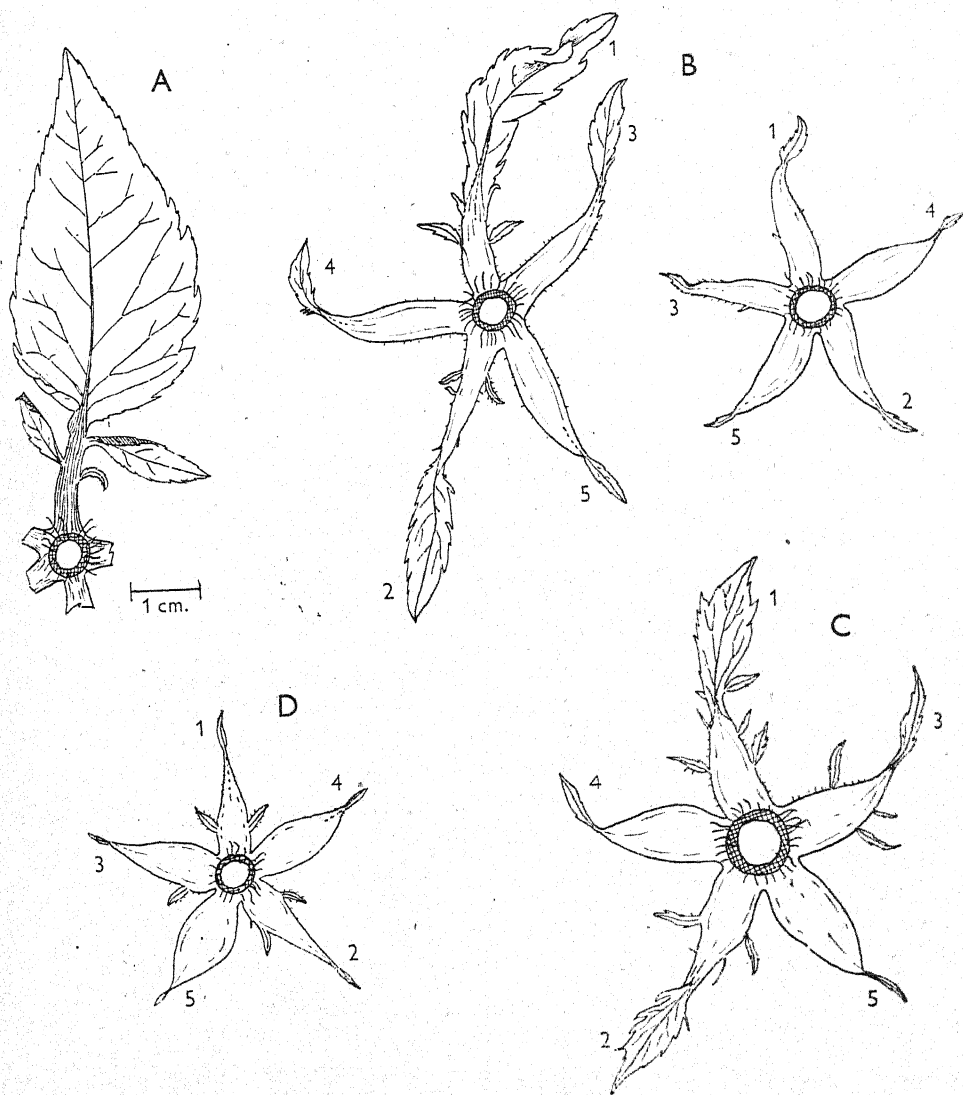

Fig. 1. Camera lucida drawings of rose calyces, from pressed specimens (all at the same scale). A. The most 'leafy' sepal, var. 'A'. B. Typical calyces from pruned (*left*) and unpruned (*right*) branches of the same bush, var. 'A'. C. A moderately 'leafy' calyx, var. 'C'. D. A calyx showing nearly the maximum degree of 'leafiness', var. 'D'.

Var. '*C*'—a distinct 'cabbage rose' type, with deep red flowers produced much less abundantly than in the preceding; foliage not red when young, flower buds quite rounded, fruits rough and prickly. The calyces (Fig. 1 C) are fairly leafy, the sepals broad at the base and with prominent lateral appendages.

Var. 'D'—flowers pink, semi-double; foliage as in 'A' and 'B', flower buds not so pointed, fruits slightly rough. In these bushes the leafy lamina of the sepals never exceeded 1 cm. in length; it remained narrow and, with the rest of the sepal, was distinctly reddish in colour. The lateral appendages (Fig. 1 D) were rather constantly paired in the first two sepals, with one only on the outer edge of the third sepal.

In all varieties, the apical lamina was easily distinguished, adaxially, by its green, leaf-like texture and venation, the rest of the sepal on this surface being thickly coated with the greyish indumentum and having little or no evident midrib. Morphologically, the sepals here described, whether 'leafy' or not, are best interpreted in terms of Croizat's (1940) concept of the 'mixed' phyllome.

Similar calyces have been well figured by Cook (1926), from roses growing under late season conditions in California.

MEASUREMENT AND COURSE OF PHYLLODY

Data were obtained entirely from dried and pressed specimens. The flowers were collected weekly from each bush, taking only those from which the petals had begun to fall. They were placed in numbered bags and allowed to wilt overnight. The stamens and any remaining petals being pulled away, the top of the receptacle, bearing the sepals, was then sliced off and pressed, the dried calyces being afterwards mounted entire with their adaxial surfaces uppermost. In recording this material, only the complete, undamaged calyces were used, preliminary '*t*' tests having demonstrated that loss or damage affected all the sepals equally, irrespective of their position or size. The degree of phyllody was expressed in terms of the average length of the leafy lamina of the first or outermost sepal in order of development.

The observations extended over a period of nearly two years, from February 1941 to January 1943. At the start, the bushes were just coming into bloom after pruning, probably, in the previous December and the phyllody was then well marked. The weekly collections were continued for the first six months consecutively and thereafter in alternate months until the bushes were again pruned early in February 1942. From the middle of the following April, the flowers were removed weekly as before but the collections were pressed and mounted only every fourth week. Certain of the bushes were again pruned in September 1942, the collections being resumed afterwards until the observations were terminated in the following January. In all, nearly 5000 flowers were collected and some 2220 measurements taken.

The course of events in the first eighteen months is summarized in Fig. 2. Varieties 'A' and 'B' showed originally a marked periodicity in the abundance of flowering, of about seven weeks duration. No such periodicity can be detected in the average degree of phyllody, which appears to be almost entirely controlled by the stage of development from pruning. Variety 'C', so far as the limited data are available, responds in the same way while variety 'D' is not noticeably affected.

In order to confirm the effect of pruning in inducing sepal phyllody, an experiment was carried out on varieties 'A' and 'B' by pruning three bushes, leaving two unpruned, and half-pruning the remainder. Both varieties were included in each treatment. The pruning, as on previous occasions, was to within a few inches of the ground: in the half-pruned bushes, one side of the bush was pruned down and the other left unpruned. Since the operation was carried out in September, and the pruned shoots were again
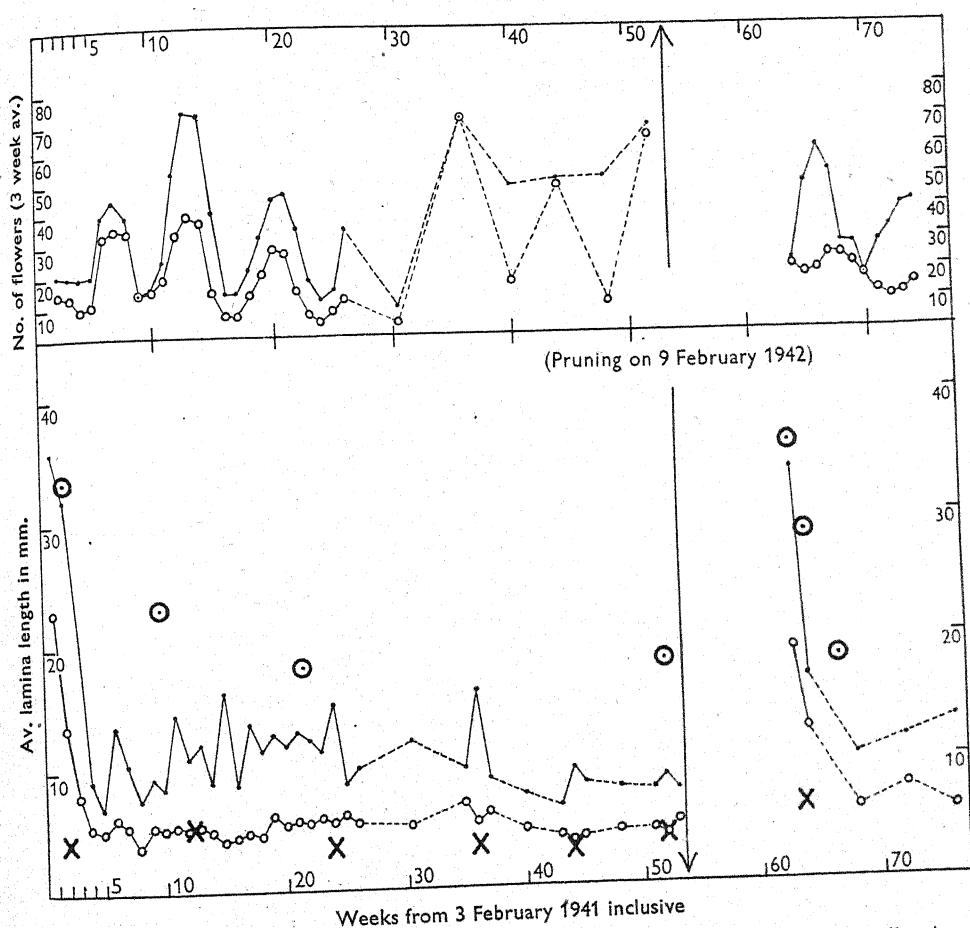
Fig. 2. Course of flowering (above) and degree of 'leafiness' (below) in the roses. The small points and circles are for varieties 'A' and 'B' respectively, in which alone sufficient data were available for the calculation of running, 3-week averages for flowering. The average lamina lengths are from unaltered, weekly records. In varieties 'C' and 'D', shown by the larger circles and crosses respectively, the data are averaged over longer intervals, as they are best available.

Table 1. *Results of pruning experiment*

(Mean lengths of lamina of outermost sepal, in mm.)

Weeks from pruning	Variety 'A'		Significance	Variety 'B'		Significance
	Pruned	Unpruned		Pruned	Unpruned	
6	—	8·9 (9)	***	18·5 (6)	4·9 (8) 4·8 (11)	**
7	26·6 (20)	6·2 (16)	*	8·2 (5)	4·8 (4)	**
8	14·9 (9)	8·9 (14)	**	8·4 (5)	3·3 (11)	**
9	13·3 (3)	7·8 (31)	**	10·5 (8)	5·6 (17)	—
10	17·4 (8)	7·5 (19)	—		4·0 (8)	
16	9·4 (22)	8·1 (19)				

Figures in brackets are the numbers of sepals measured; the significance levels of the differences, by *t*-test, are: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

coming into bloom by November, the season of the year was quite different from either of the two previous occasions (February 1941, April 1942) on which the bushes were observed at this stage. The results of the experiment (Table 1, Fig. 1 B) were clear-cut, especially in the half-pruned bushes where the flowers on the two sides of the bush were in close juxtaposition. The measurements summarized in the table showed that the effect of pruning persisted for at least four weeks after flowering started on the pruned shoots but could no longer be detected by the tenth week.

<div style="text-align:center">QUANTITATIVE INTERPRETATION</div>

Sepal phyllody, as here understood, is a quantitative change which, alike among the different sepals of the individual calyx as between the different calyces developed successively during recovery from pruning, shows an imperceptible gradation to the normal. Thus, it becomes of interest to discover the common basis, if any, of these two processes. Preliminary measurements readily showed that there was no allometric relationship between the 'lamina', whether enlarged or otherwise, and the basal portion of the sepal. The relative lengths of the sepals in their order of development were then examined, when it was found that these tended to decrease in geometric progression. Taking the 'lamina' lengths alone confirmed the tendency and it was on account of this relationship that the degree of phyllody or leafiness of the calyx as a whole could be expressed, as above, in terms of the length of the leafy apex of the outermost sepal.

There is, accordingly, a constant average 'dilution factor' (common ratio) determining the reduction in lamina length between any two sepals developed consecutively. In other words, these lengths when averaged as logarithms against their respective positions as determined from the phyllotaxy give a straight line relationship. This result is far-reaching, since it provides a common measure of relationship between the sepals, irrespective of their absolute size—i.e. it is equally applicable to normal and to 'leafy' calyces.

Fig. 3 shows the logarithmic plotting of the data from forty complete calyces, ten from each variety, selected five at a time from before and after pruning to include as wide a range of types as possible. The points for the five positions of phyllotaxy give a close fit to a straight line with a regression of b (log y on x) $= -0.130$, corresponding to a common ratio of 0.741. (A second test, on twelve other calyces of 'leafy' and normal type, gave a value of $b = -0.146$, or a ratio of 0.714, not significantly different from the preceding.) From the logarithmic relationship, a curve can be constructed of the type y (lamina length) $= Ce^{-rx}$, where x is the unit of phyllotaxy, i.e. the plastochron. The individual calyces are then fitted to the curve from the geometric means of their lamina lengths. The figure shows that, as compared with the closeness of fit of the averaged, logarithmic data, there is now a considerable divergence between the observed measurements and the calculated curve. Two possible reasons for this were suggested by a further examination of the data, namely, that the common ratio may, in fact, increase with increasing 'leafiness' and that it may also be significantly higher in variety 'C' (0.690) than in any of the others (av. 0.759). Moreover, individual exceptions may be found where, for example, the length of the second sepal may equal or exceed that of the first. These considerations, however, do not affect the general validity of the conclusion that the lamina lengths of successive sepals are, on the average, in a geometric

series of which the mean common ratio is rather more than 0·7—the leafiness is, as it were, 'diluted' by an equal amount at each interval of phyllotaxy.

Further confirmation of the logarithmic relationship governing the same type of sepal phyllody in roses was obtained from Cook's (1926, figs. 10–12) illustrations in which,
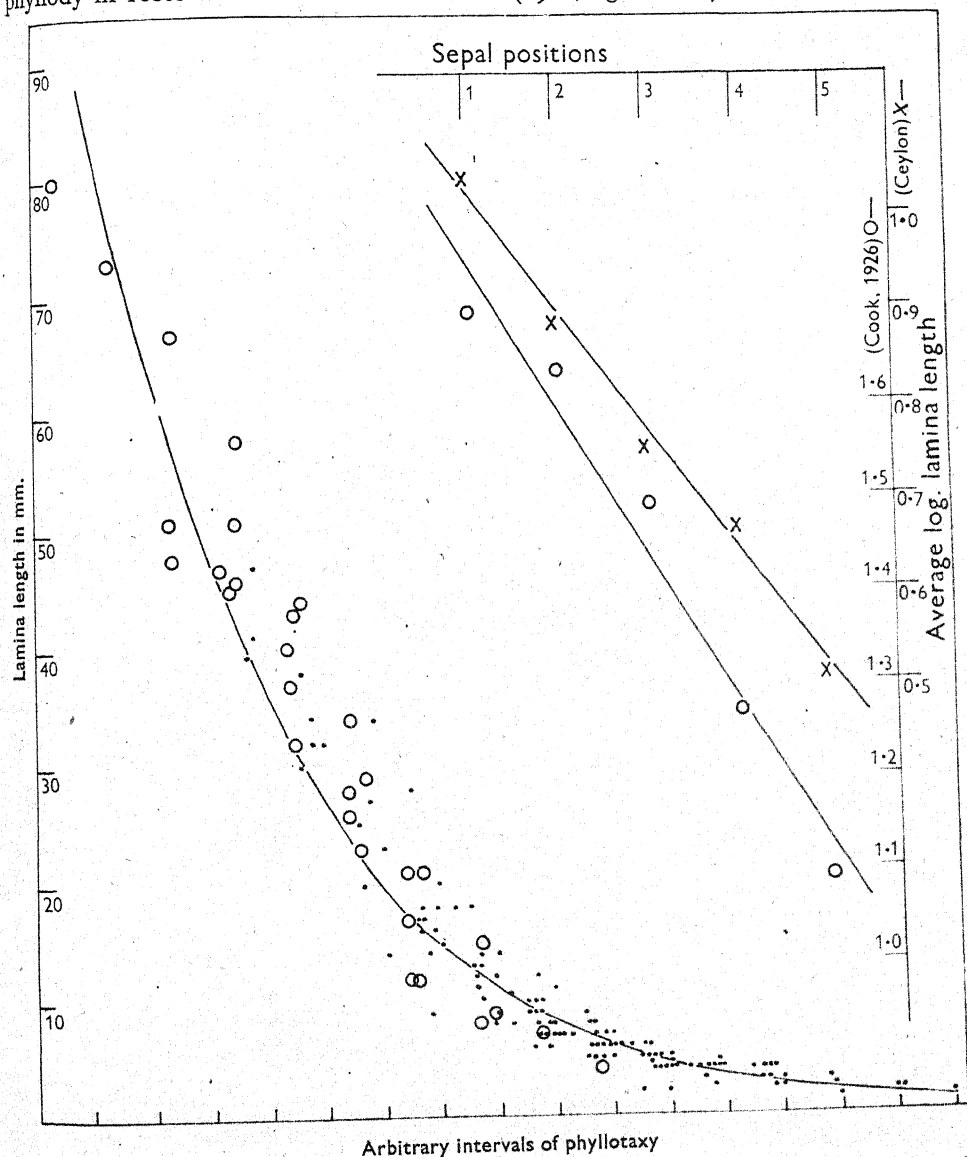

Fig. 3. Logarithmic plotting of lamina lengths in rose calyces, original data, ×—×, and from Cook (1926), ○—○. The curve is from the former, in which $b = -0.130$. (For further explanation, see text.)

among others, six complete calyces are figured. The measurements from these are shown also in Fig. 3. Considering the small numbers available (i.e. thirty sepals in all) they give a satisfactorily close fit to a logarithmic regression of $b = -0.159$, or a geometric common ratio of 0·694, not significantly different from the present Ceylon estimate of 0·714.

Other examples ·

The demonstration of the geometric series controlling the leafiness of successive sepals in the rose calyx suggested the further application of the idea to two other examples which had previously come under the writer's notice and for which the necessary detailed measurements (unpublished) were still available. These comprise a straightforward and quite homologous instance of sepal phyllody in primroses and the symptoms, morphologically distinct but effectively analogous, of smut infection in the grass, *Elymus arenarius* L.
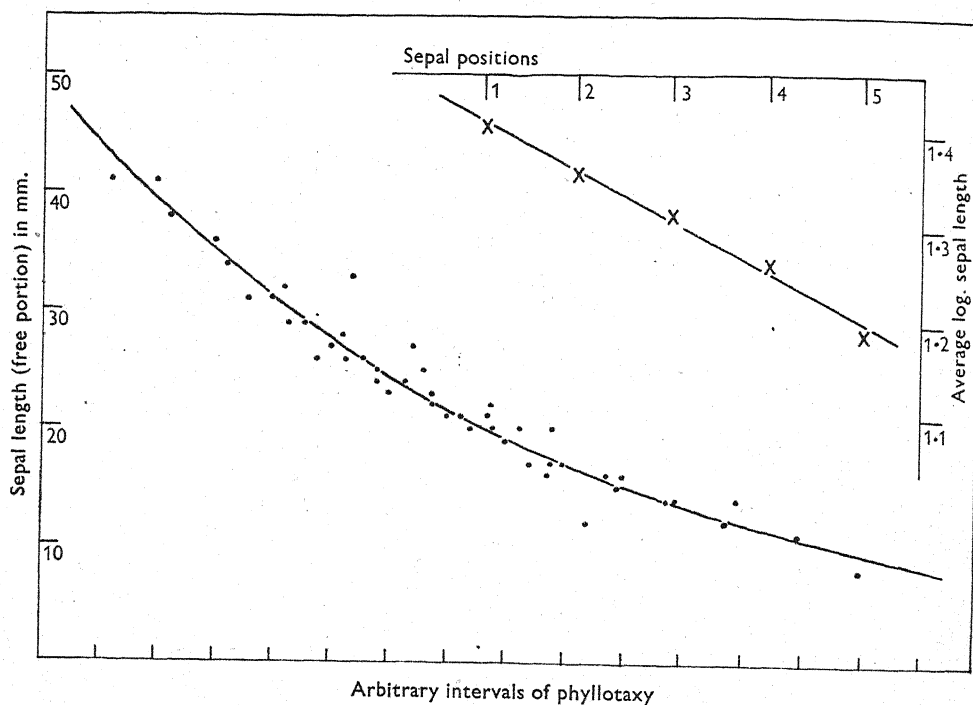

Fig. 4. Logarithmic plotting of free sepal length in primrose calyces, with the calculated curve.
(For further explanation, see text.)

The primroses (*Primula vulgaris* Huds.) were grown in Ceylon and the sepal phyllody developed under conditions suggestive of the effect of an increase in mean temperature following transplanting from a region of higher elevation (Bond, 1941). Scale drawings of ten complete calyces were available, four of which were previously published (Bond, 1941, figs. 1 A–D). The calyx is toothed at the apex but the sepals cannot be said normally to comprise a laminar appendage, as in the rose. Thus, measurements were confined to the free portions of the sepals, whether these were leafy or not. Arranging the sepals in order, as far as this could be determined, and averaging by logarithms again gave a close fit (Fig. 4) to a straight line with a regression of $b = -0.0514$ which corresponds to a common ratio of the geometric series of 0.888. The figure also shows the unaltered data, fitted by their geometric means to the curve deduced from the logarithmic regression. On the whole, the agreement is closer than that given by the rose calyces.

Details of the second example, the symptoms induced in *Elymus arenarius* L. by the smut fungus *Ustilago hypodytes* (Schlecht.) Fries, are given by Bond (1940). The inflorescence region of the culm becomes greatly elongated and leafy bract-like appendages develop which are normally represented, at the basal node of the spike, by the 'collar leaf' and elsewhere by the 'rachilla flap' in Arber's (1934) terminology—abortive structures with no vascular supply which are scarcely separable from the main axis (Fig. 5). When enlarged under the influence of the fungus, they become vascular and


5 mm.
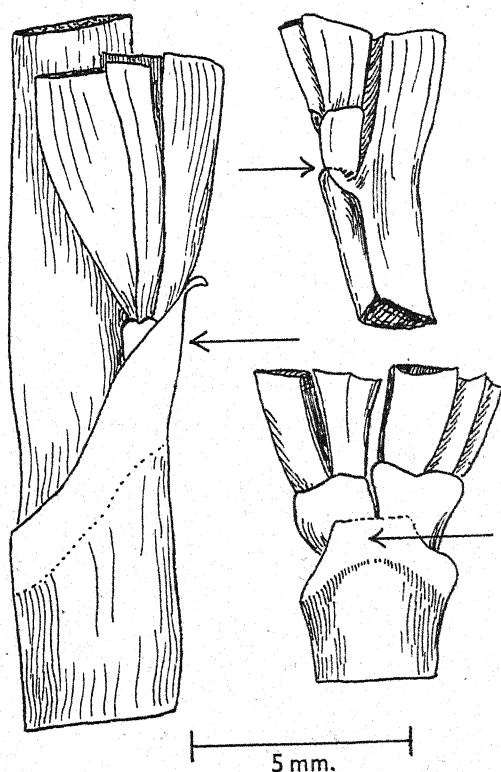
Fig. 5. Drawings of the lowest (*left*) and an intermediate (*right*) node of the healthy inflorescence of *Elymus arenarius*. The glumes are cut short. The structures marked by the arrows correspond to the 'collar leaf' and 'rachilla flap' respectively of Arber's terminology. In the diseased plants, these develop into long, leafy bracts.

resemble the normal leaf-sheaths in general appearance and structure, with a maximum length of about 40 cm. Data were available in the measurements of eleven culms collected at Aberdeen, Scotland, in the summer of 1938. Only the lowest six appendages and their associated internodes, in which growth had ceased, were included. (The internode is that *above* the node from which the appendage itself arises.) Their lengths decrease from below upwards, again, as shown in Fig. 6, in a geometric series with a mean common ratio of 0·723. The values for the bracts ($b = -0·137$, or

c.r. of 0·729) and their internodes ($b = -0·144$, or c.r. of 0·718) were not significantly different.
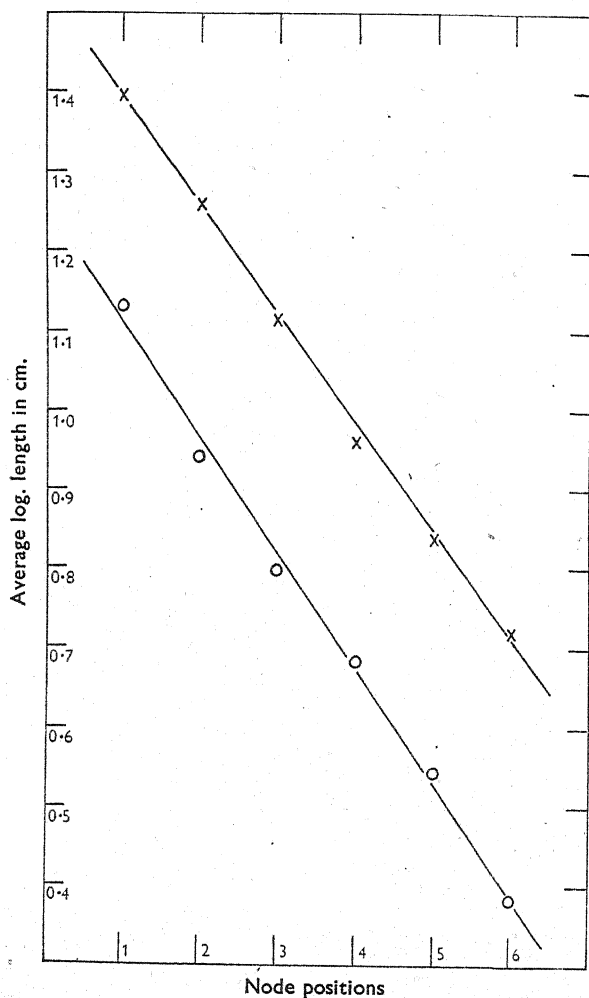
Fig. 6. Logarithmic plotting of mature bract (×—×) and internode (○—○) lengths for the first six nodes of the diseased *Elymus arenarius* inflorescences.

DISCUSSION

Burkill (1935) and others speak of sepal phyllody and analogous phenomena as resulting from the 'invasion of vegetative tendencies' into the inflorescence region. It now seems likely that this invading tendency is progressively eliminated or diluted in a logarithmic fashion, being decreased in proportion at each plastochron or corresponding morphological interval. The fact that a similar relationship holds good for the 'leafy' as for the normal calyces suggests that the progressive decline in leafiness in the rose calyces after pruning is itself subject to the same general principle. That this is actually so, at least for the first five weeks (after which the effect is obscured by apparently random fluctuations, as shown in Fig. 2), was established by averaging all the available data and plotting

logarithmically, as before. Calculated as a linear regression, the value of $b = -0.126$ was significant at the 1% level of probability. Here again is a 'dilution' series with a common ratio of 0.75 per week. The pruning effect itself indicates that the 'vegetative tendency' is no mere phenotypic expression but that it has genuine causal significance. Vegetative growth is known to be particularly vigorous in the period of recovery from pruning and, in the Ceylon climate, this effect is presumably even more marked than usual. Here also is a probable explanation of the effect of temperature suggested previously by the writer (1941) to account for the behaviour of the primrose flowers in Ceylon, and similarly employed by many other writers on teratology—the increase in temperature leading to an acceleration in growth. Again, in the diseased *Elymus* plants, vegetative vigour is increased in the sense (Bond, 1940) that growth of the rhizomes is no longer interrupted by the normal periods of quiescence and that the erect axes are frequently proliferated from the base as well as greatly lengthened in the inflorescence region.

The view that the phenomena here described are indeed the result of a vegetative impulse, associated with an abnormal vigour of growth and regularly and successively 'diluted' during the reproductive phase, leads naturally to the suggestion of control through the agency of hormones. In this connexion, Anderson and de Winton's (1935) discussion of the genetically induced leafy calyx of *Primula sinensis* is particularly apposite, and it is surprising that these authors' views on the balance between the vegetative and reproductive phases have apparently been so largely neglected in recent studies on 'correlative inhibition' and related fields (Went & Thimann, 1937; van Overbeek, 1944). An early reference quoted by Masters (1869, p. 168) on the presumptive transformation of a flower bud to a leaf bud by the removal of the carpel initials is of interest here. A hormonal interpretation of the *Elymus* symptoms is suggested by the known ability of various pathogenic fungi to produce auxins. In this instance, the mycelium is especially abundant in the buds (Bond, 1940, p. 334) so that any products of fungal growth, including hormones, might be expected to move predominantly *downwards*. A downward movement of the leaf-inhibitor from the reproductive apex was postulated by Anderson & de Winton (1935). On the other hand, the association with vegetative vigour, so clearly shown by the sepal phyllody in roses, is suggestive of an *upward* movement of a promoting factor. In this connexion, it should be noted that the 'dilution' effect would be the same either way—the successive, proportionate dilution of a promoting factor can equally be represented as the increase of an inhibitor. The fact that, as Snow (1940) has proved, a hormone controlling correlative inhibition can move alike in both directions will also need to be taken into account. On the whole, the period of recovery from pruning, and probably any phase of abnormally rapid vegetative growth, is marked by a general upward trend of organic solutes as is seen, for example, in the extension of plant virus symptoms under these conditions (Bennett, 1940; Hildebrand, 1943). On either interpretation of the mechanism of hormonal control, such an upward trend would be sufficient to induce the phenomena here described.

SUMMARY

Roses in cultivation in Ceylon frequently exhibit a condition of sepal phyllody consisting in the enlargement of the normal, apical appendage of the sepal to form a leafy lamina, up to 5 cm. or more in length, the calyces, and flowers generally, being otherwise

normal. Continuous observation over a period of two years showed that the condition, though in part a varietal character, was principally controlled by the stage in development from pruning, being most in evidence thereafter during the first five weeks' flowering.

The degree of leafiness in the individual sepals, measured by their 'lamina' lengths, decreases in a geometric series according to the position as determined by the two-fifth phyllotaxy, the outermost sepal being the most leafy and the innermost the least. This relationship applies equally to the normal as to the 'leafy' calyces, the average common ratio of the geometric series for roses of all four types examined being rather higher than 0·7.

A similar 'dilution' of the tendency to 'leafiness' at successive plastochrons was demonstrated also from unpublished data for sepal phyllody in primroses (*Primula vulgaris*) in Ceylon and for the abnormal inflorescences resulting from smut infection in the grass *Elymus arenarius* in Britain.

The results are discussed in relation to the probable effect of hormones in controlling the vigour of growth and the balance between the normal reproductive and vegetative tendencies.

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EFFECT OF CARBON DIOXIDE UPON CARBON DIOXIDE PRODUCTION IN THE ABSENCE OF OXYGEN

BY FRANKLIN KIDD

Low Temperature Research Station, Cambridge

AND CYRIL WEST

Ditton Laboratory, East Malling, Kent

(With 1 figure in the text)

Unpublished results obtained by J. K. Hardy (1939) indicate that, under conditions in which carbon dioxide was allowed to accumulate in the atmosphere as a result of the activity of apples when enclosed in gas-tight containers in the absence of oxygen, there was no evidence, over a short period, of a fall in the rate of carbon dioxide production with increasing concentrations of carbon dioxide in the atmosphere, and hence in the tissues. Previous results (Kidd & West, 1937) had shown that in air the rate of carbon dioxide production of apples during their post-climacteric phase is progressively depressed with rising concentration of carbon dioxide in the atmosphere, and hence in the tissues. If aerobic carbon dioxide production is depressed by the presence of carbon dioxide but anaerobic carbon dioxide production is not depressed, the fact must be of interest in connexion with the intermediate theories of metabolism of the respiratory process.

Experiments have been conducted to check Hardy's results by a method in which the fruits were exposed to a relatively constant pressure of carbon dioxide over a longer period. The method used for the estimation of carbon dioxide production by apples in the presence of carbon dioxide in air has already been described (Kidd & West, 1933). The experiments were carried out at 10° C.

Three samples of Bramley's Seedling apples were obtained on 29 September 1939. In the case of two of these samples (nos. 1 and 2) the fruit was pre-climacteric, and in the other (no. 3) post-climacteric. The respiratory history of these three samples is shown in Fig. 1 (top). The first sample (no. 1) was exposed, at the outset, to an atmosphere of pure nitrogen, and it can be seen, by comparing the results with those of the second sample (no. 2), which was in air, that transference from air to nitrogen had very little effect on the rate of carbon dioxide production. Both these samples were pre-climacteric. At the point marked *A* the sample in nitrogen was transferred to an atmosphere of 10% carbon dioxide in nitrogen from which all traces of oxygen had been removed. The carbon dioxide caused a slight, though definite, depression in respiratory activity. At *B* when the sample was returned to nitrogen without carbon dioxide, oxygen still being absent, the respiratory activity rose again slightly.

The second sample (no. 2), which was in air at the outset, began to show its climacteric rise after about 7 days. On the 10th day, before the climacteric rise had fully developed, it was transferred to nitrogen at the point *C*. The respiratory activity in nitrogen remained on the pre-climacteric level. At the point *D* when it was transferred to 10% carbon

dioxide in nitrogen, the respiratory activity fell slightly. The line *CEH* represents the behaviour to be expected, if this sample had not been transferred to nitrogen at *C*, but had remained in air.

The third sample (no. 3) was placed in nitrogen at the outset. The respiratory activity was high and indicated that the fruit was post-climacteric. Its record is therefore shown in the figure as starting at the point *E* on the peak of the climacteric rise in air. In this
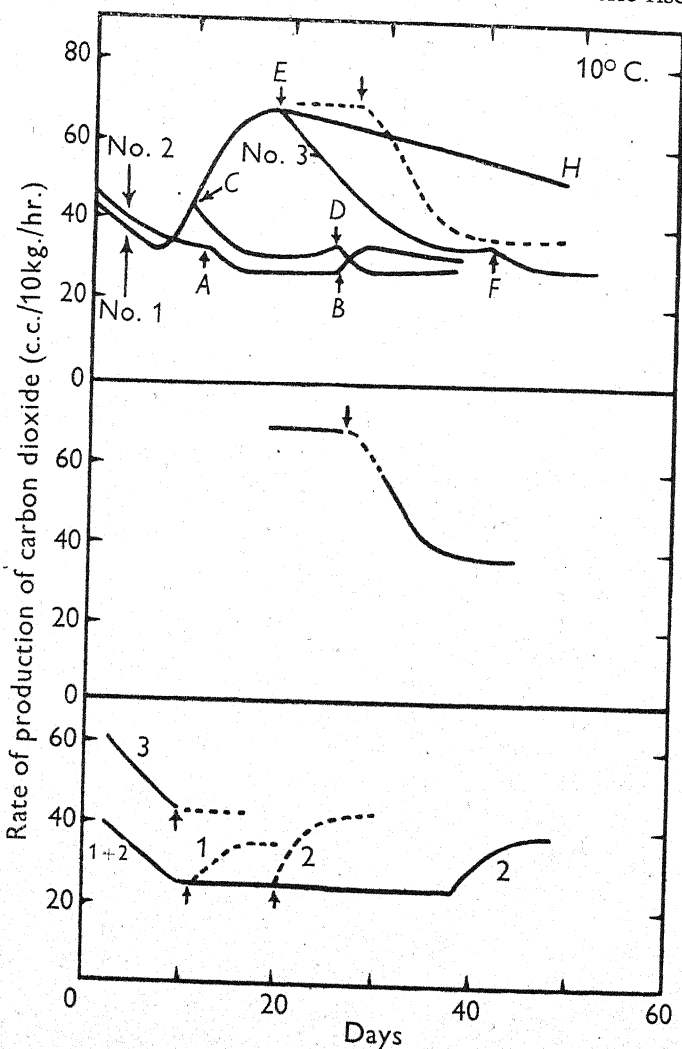

Fig. 1. Respiratory activity of Bramley's Seedling apples, as affected by carbon dioxide in the absence of, and in the presence of, oxygen. (For explanation, see text.)

case there was a very marked fall in respiratory activity lasting 10–15 days, but the final level reached was approximately the same as that of the pre-climacteric fruit. This sample was then transferred, at the point *F*, to 10% carbon dioxide in nitrogen when the activity fell slightly.

In all three cases of the transference from nitrogen to 10% carbon dioxide in nitrogen the fall in respiratory activity was about the same, namely, about 20%.

When the fruit was transferred to nitrogen from air in the pre-climacteric phase (nos. 1 and 2), little change in the rate of carbon dioxide production was observed; moreover, it seemed probable that the climacteric phase had not occurred up to the termination of the experiment.

On the other hand, when the transfer to nitrogen from air was made at the peak of the climacteric rise, the respiratory activity fell over a fairly long period to a value characteristic, apparently, of pre-climacteric fruit.

It seemed desirable to apply some test to the apples in each case to ascertain whether they were in a pre- or post-climacteric condition at the termination of the treatments described above. Accordingly, a few fruits from each of the samples 1, 2 and 3 were placed in containers in air and their respiratory activity followed for a further period. Fruit from samples 1 and 2, which was believed to be pre-climacteric, had a lower level of activity than that of sample 3, which was believed to be post-climacteric (Fig. 1 (bottom)). Moreover, when treated with ethylene after a few days it was found that apples from samples 1 and 2 showed a rise in respiratory activity such as is brought about by the treatment of pre-climacteric fruit with ethylene. Fruits from sample 3, on the other hand, when treated with ethylene, showed no rise. One fruit of sample 2 was kept under observation without ethylene treatment, and this fruit eventually showed what appeared to be the normal climacteric rise. These results are shown in Fig. 1 (bottom). The vertical arrows indicate the points in time at which ethylene stimulation was applied. The broken lines trace the behaviour after treatment with ethylene.

It seemed also desirable to test, on similar fruit, the extent of the reduction in activity produced by 10% carbon dioxide in air. This final experiment was carried out with fruit which had been stored at 4° C. while the other experiments were being conducted, and the result is shown in Fig. 1 (centre). Carbon dioxide was applied at the point in time marked by a vertical arrow. The reduction in respiratory activity in air produced by 10% carbon dioxide was of the order of 45%. The result is also shown in Fig. 1 (top) as a broken line. The value in air before the application of 10% carbon dioxide is a post-climacteric one, as was to be expected.

The work described above was carried out as part of the research programme of the Food Investigation Board and is published by permission of the Department of Scientific and Industrial Research.

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REVIEWS

American Botany, 1873–1892. *Decades of Transition*. By ANDREW DENNY RODGERS III.
Princeton University Press; London: Humphrey Milford, Oxford University
Press. 1944. Pp. 340. English price 25*s*. net.

A good deal has been said in recent years on the value in teaching of the history of science as a
whole. Many of the arguments used would apply equally within the domain of botanical teaching.
There is, however, a lack of modern text-books on the subject and this may be the most important
reason why it is, at least in England, largely avoided by students and teachers. It would appear
from recent publications (see especially those of *Chronica Botanica*) that the history of botany is
becoming a very live issue in the United States. Andrew Denny Rodgers III, in addition to the
book now under notice, has written works on William Starling Sullivant, John Merle Coulter, and
John Torrey. These, together with other historical and biographical accounts published or contem-
plated, should give ample material for a concise account of the history of botany in America up to
recent times.

The botanical historian is obviously faced with a major difficulty in deciding how to arrange his
materials. A strict chronological sequence of happenings would be little more than a catalogue of
facts lacking interpretation. A biographical arrangement would result in a series of biographies
rather than a coherent history. A first division into botanical subjects would appear to have most
advantages so long as the influences one subject exerts on another be kept in mind. Within each
subject the record of increasing knowledge must obviously be approximately chronological
although this must be balanced by such biographical data as will indicate clearly the debt owed to
outstanding individuals.

American Botany, 1873–1892, is given the subtitle *Decades of Transition* to indicate that it covers
the twenty years during which, in America, botany changed from being almost purely systematic
into a largely experimental science. In 1873 Torrey and Sullivant died and Asa Gray was left as
the undisputed leader of botany in America. It follows that this history is dominated by the
activities of Asa Gray, till his death in 1888, and his connexions with other great American botanists
of this period: Engelmann, Watson, Parry, Palmer, Bessey, Coulter, Farlow, Eaton, Lemmon,
Lesquereux, Pringle, Trelease, Vasey, Sargent, Bailey, and others. Though the period did see
botany extend its boundaries very widely in regard both to subject-matter and methods, Asa Gray
remained essentially a taxonomist, and the present volume is mainly a record of the continued
exploration of the existing flora of the United States, with extensions to Canada, Mexico, and,
latterly, by Rusby, to South America. One exception to this last generalization is the work on
Mesozoic and Cainozoic fossil floras by Lesquereux. Asa Gray, too, was not content only to
describe and name but, as is well known, did much to improve the general standard and teaching
of morphology and, in another direction, put forward reasoned explanations of the phytogeo-
graphical problems which his floristic studies did so much to reveal.

Our author has evidently taken much trouble in consulting original sources, and a very large
number of letters are here published for the first time. It is probable that some of the faults of
treatment which seem noticeable to the reviewer would be considered of little importance by
American botanists. The chapter headings do not always indicate their contents fairly. No maps
or plans are provided, and the political geography of the United States has changed in various
respects between this 'transition period' and the present day, while adequate historical atlases of
the U.S.A. are not generally available to English readers. There is little or no link-up between the
general history of the country and that of botanical development and exploration. Some of the
letters could well have been left out, and the space saved could have been used to make a more
connected and interesting story, though there are a few human, and even unintentionally amusing,
touches. One cannot refrain from quoting the following (p. 54): 'Greene was for two years—
1862–1864—a private in the Thirteenth Wisconsin Infantry. While on guard and doing patrol
duties of one sort or another, as opportunity permitted, he studied Alphonso Wood's *Class Book
of Botany* and succeeded in botanizing in Kentucky, Tennessee, and Alabama.' There is an ade-
quate index, but an appendix giving in a concise form biographical details of the botanists mentioned
in the text would have been very helpful.

English botanists will note with pleasure the accounts of the close connexions between Asa Gray

and the Royal Botanic Gardens, Kew, and especially with Sir Joseph Hooker. Attention may be called to the great series of letters preserved at Kew which, judging from the 'acknowledgments', does not appear to have been consulted in the preparation of this book. The author has, however, evidently taken great care in checking his facts and quotations, and the volume will prove useful for consultation by all working on North American botany. One also receives the impression, no doubt correctly, of the great energy, activity, and whole-hearted enthusiasm with which the botanical exploration of a newly opened up subcontinent was undertaken. Nevertheless, the some-what discursive arrangement of the materials does not make it easy for the reader to keep the main trends clearly in mind.

W. B. TURRILL

Flora of Illinois. By GEORGE NEVILLE JONES. 9×6 in. 318 pp., 2 maps in text. Notre Dame, Ind.: The University Press. April 1945. The American Midland Naturalist, Monograph No. 2. $4.00 cloth bound, post paid.

The word 'Flora', even as used in systematic botany for a published account of the plants of a geographically or politically delimited area, covers varied productions. The mighty tomes of Martius's *Flora Brasiliensis*, the *Flora Orientalis* of Boissier, the *Flora Capensis*, the *Flora of Tropical Africa*, the *North American Flora* (not yet completed), and others almost of the nature of periodicals contrast with the compact single volumes of 'Bentham and Hooker', Babbington, and innumerable 'local' floras. It is not only in format, however, that we find lack of uniformity, but also, and even more, in contents. Some floras contain more or less full descriptions and ranges, with or without keys and illustrations. Most British 'county floras' are essentially lists of species with the localities under every one where the plant so named has been found within the county. The relative merits and demerits of floras covering larger or smaller areas can be nicely argued. The modern tendency is towards the latter, but there are some exceptions, as the new *Flora of U.S.S.R.*

Floras have been published, or are in course of publication, for many of the states of the U.S.A. Most often these have systematic descriptions of the taxonomic units accepted and perhaps approxi-mate, on the whole, to Hooker's *Student's Flora of the British Isles* rather than to our county floras. The *Flora of Illinois*, here under notice, has a short introduction followed by keys to the families, genera, and species of the vascular plants found in the State. There are no descriptions or figures and only outline ranges are given. The keys appear to have been very carefully prepared, and the clear numbering and indentation of the dichotomies makes them easy to use. The volume is one that should be extremely valuable to field workers, but it would surely have been much more handy had its size been reduced so that it would fit into an average coat pocket and its weight lessened by the use of thinner and less heavily glazed paper.

Illinois is part of the Great Central Plain of North America and has an area of approximately 57,926 square miles. The native species are mostly of southern affinities, and the boreal element is extremely small. During the Glacial Period (with four advances of the ice-sheet), Illinois was heavily glaciated, and only three portions of the State were untouched by the Pleistocene glaciation. Extensive forests and grasslands formerly covered the entire region. Much of the surface is now under cultivation. The original prairies in northern and central Illinois have now all but vanished, and their natural vegetation has disappeared except along roadsides and railroads. The larger forests are in the southern counties and are composed almost entirely of hardwoods. There are large sand and sandy loam areas in the northern part of the State. Though the vegetation has been so much modified by man since colonization from the east, the flora remains rich. 2124 species of vascular plants are recorded of which 1786 are indigenous. There are 302 species of trees and shrubs (*Salix* 17, *Quercus* 19, *Crataegus* 14). Compositae is the largest family with 243 species and *Carex* the largest genus with 114 species. There are 215 species of grasses, of which 166 are native, *Panicum* being the largest genus in the family and having 36 species. For a prairie State the numbers of vascular cryptogams (63 species) and of woody plants are high.

The vegetation is rather sharply differentiated into prairie and forest, each including a number of communities. A map is provided showing the botanical divisions based principally upon the broader topographical features. The area affected by the recent (Wisconsin) glaciation is mostly treeless, and extensive areas of upland prairie formerly occurred in the western division. An outline account of the soils and vegetation of the eight divisions is given. In addition, there are a map of the counties, a glossary, a bibliography, an author index, and an index of plant names.

W. B. TURRILL

Fragmenta Papuana. [*Observations of a Naturalist in Netherlands New Guinea.*] By H. J. LAM. Translated from the Dutch by LILY M. PERRY, with a Foreword by E. D. MERRILL. 10 × 7 in. Pp. 1–196, with 2 maps and 32 text-figures. Sargentia (A continuation of the Contributions from the Arnold Arboretum of Harvard University), 5. The Arnold Arboretum, Jamaica Plain, Mass., U.S.A. 1945. Price $3.

New Guinea is one of the most interesting countries in the world to the botanist because of the great richness and variety of its flora and the wealth of strange forms of plant life it contains, many more of which doubtless still remain to be discovered. New Guinea too has perhaps the largest remaining area of truly natural vegetation in the world, and the rapid change from hot equatorial lowlands to glaciers and permanent snowfields gives unique opportunities to the ecologist interested in the altitudinal zonation of vegetation.

Prof. Lam was botanist on the van Overeem Expedition which in 1920–1 ascended the Mamberamo river from the north coast, climbed the 3580 m. high Doorman-top and explored the remote Dika and Toli valleys to the south of it, where a previously unknown tribe of mountain Papuans, the Timorini, was discovered. The route of the expedition crossed the *Meervlakte*, a huge expanse of open water, reed beds and swamp forest occupying an old lake basin, and gave ample opportunities for studying all the altitudinal zones of vegetation on the mountains from the lowland rain forest to the dwarf heath-like vegetation which covers the summit of Doorman-top. On his return, as well as describing his collections, Prof. Lam wrote a series of seven general articles in the *Natuurkundig Tijdschrift voor Nederlandsch-Indië*, of which this work is the translation.

The articles include a chronicle of the expedition and a history of previous explorations, meteorological observations, descriptions of the flora and plant communities met with and, in the last section, an account of the land and people of the Dika and Toli valleys. The text is illustrated by a number of sketches and diagrams, including schematic profiles to show the structure of the lowland rain forest and the 'mossy forest' respectively. Prof. Lam's photographs are not reproduced here, but are readily available in his 'Vegetationsbilder aus dem Innern von Neu-Guinea' (Schenck and Karsten's *Vegetationsbilder*, Reihe 15, Hefte 5–7, 1923–4). The articles are no bald recital of names and localities; they give a vivid impression of the whole region and of the author's delight in superbly beautiful natural surroundings. Useful discussions of the genetic plant geography of the region and of the problem of the xerophytism of the high mountain flora are included. The account of the ruderal flora of the Dika and Toli valleys is of special interest because of the extreme isolation of the area. The valleys are separated from the coast by hundreds of kilometres of virgin rain forest and their inhabitants have only very few contacts with the outside world.)

The translation renders the sense of the original on the whole adequately, though a few sentences are misleading or incomprehensible (e.g. in the last paragraph on p. 84 'under the high trees' should presumably have been translated 'among the high trees'), but it is perhaps ungrateful to mention these defects in view of the great service which has been done in making this important and delightful work accessible to the English-speaking public.   P. W. RICHARDS

Root Disease Fungi. By S. D. GARRETT. 9 × 6 in., 177 pp. Chronica Botanica Co., Waltham, Mass.; Wm. Dawson and Sons, Ltd., London, W. 1. $4·50.

Most of the soil fungi that cause important root diseases in plants are specialized parasites and are found in the soil only in relation to the presence or past presence of suitable host plants. Very few of them appear to be able to live freely as saprophytes; when the host plants die the fungi disappear unless a new host is found, but this disappearance is sometimes slow. Dr Garrett's book contains an ecological study of these specialized parasites and a discussion of the principles underlying the various methods of controlling the diseases which they cause. No attempt has been made to deal comprehensively with all root-infecting fungi nor with all root diseases; attention is focused on a restricted but representative number of fungi causing diseases of notable economic importance, diseases which have been the subject of close and careful study. In discussing the ecological complex of fungus and soil environment, examples are usually drawn from this well-attested material, but the book has not been unbalanced by applying this selection too rigidly.

The Introduction is in fact a summary of the information given and the conclusions reached in the rest of the book; this is followed by a brief general essay on soil fungi and a clear and concise summary of information on mycorrhiza. Dr Garrett then discusses the methods by which fungi

spread through the soil from one plant to another, drawing a careful distinction between spread of the fungus and spread of the disease. Three chapters are devoted to the influence of soil conditions (temperature, moisture content, texture, reaction, organic content and concentration of plant nutrients) upon the occurrence of soil-borne diseases. The discussion centres around the thesis that soil conditions will exert the greatest direct influence upon those fungi that spread chiefly by mycelium external to the host, and only an indirect influence, through host physiology, upon the fungi which spread only inside the host.

The next section deals with the survival of the root-infecting fungi between periods of active parasitism. Survival by free saprophytism, by limited saprophytic activity in tissues originally invaded as a parasite, by resting spores and sclerotia is discussed, and the influence of varying environmental conditions upon the time of survival is analysed. This leads on naturally to the question of control, and the second half of the book is devoted to an account of the control methods used and a correlation of the effectiveness of the methods with their fundamental basis—the autecology of the fungi concerned. The control of root disease in field crops is discussed in this way in three chapters dealing with crop rotation, the elimination of disease by methods of plant sanitation, and the manipulation of soil conditions. The next section is of particular interest, being devoted to a survey of root-disease control in plantations under tropical conditions. In this survey the recent outstanding discoveries made by Napper in the control of root diseases in young and old plantations of rubber in Malaya, and by Leach in the disease of tea caused by *Armillaria mellea*, are clearly described in great detail and are correlated with the pioneer work of Petch. By contrast with the rest of the book, the final chapter on control under glasshouse conditions is slightly disappointing, being mainly a description of methods of effecting satisfactory sterilization of soil.

This authoritative and very readable book by one of the foremost workers in this field of research will be widely welcomed. Its strong practical bias should recommend it to the grower of crops who is interested in the why and wherefore. To the plant ecologist it presents work and problems in a possibly unknown field which cannot fail to be of interest, and for the pathologist it contains a wealth of collected and ordered information which previously was available only in very scattered form. It contains 16 pages of references as well as comprehensive subject and author indexes. This is the first volume of Chronica Botanica's new series 'Annales Cryptogamici et Phytopathologici' and is of the same format as the 'New Series of Plant Science Books'. G. METCALFE

Structure and Reproduction of the Algae. Vol. II. *Phaeophyceae, Rhodophyceae, Myxophyceae.* By FELIX E. FRITSCH. Pp. xiv + 939, frontispiece, 336 text-figs., 2 maps. Cambridge: University Press. 1945. 50s.

It is most unusual when for one of the great groups of plants someone really adequately learned can be found willing to undertake the immense task of ordering the knowledge of the day and presenting an epitomy of it for the service of his colleagues. This is just what Prof. Fritsch has completed for certain phases of our knowledge of the great group of algae. Fritsch will probably be the last man able by his own efforts to compile a comprehensive account of the greater part of our knowledge of the algae, for the literature has grown so enormously of recent years that it will be impracticable for one man to cover the whole field. Only once before has this been done on a tolerably adequate scale, by F. Oltmanns (*Morphologie u. Biologie der Algen*, 1904–5, 2nd ed. 1922–3), though G. S. West (*Algae*, vol. I, 1916) began a less detailed account which he was unable to complete. The two volumes are alike in character in that they form an essentially advanced reference work. The amount of material incorporated is stupendous, and most elaborately documented; it is evident that the utmost diligence was exercised to include all significant work up to the time of publication. The present portion of Fritsch's account of the algae comprises the groups remaining after his first volume, with a Foreword on general matters. These groups are dealt with in the same meticulous detail with which he earlier discussed the Chlorophyceae and other groups (1935). For each of the three classes there are several excellent pages of general information regarding cell structure, vegetative organization, food reserves and reproduction, and then detailed analyses of the special morphology and reproduction of each family.

In the present book by intent morphology and reproduction are stressed, taxonomy only appears as is necessary to organize the material, and ecology, physiology and like topics are only incidentally treated. It is always difficult in compiling a book of this type, where for many genera no recent studies exist, to give a balanced and authoritative account, neither neglecting what was good in older works nor maintaining old errors, while utilizing wherever possible the modern researches. Most writers in systematic morphology have been content to select one well-known example to

typify a family or genus, while neglecting the bulk of the literature; Fritsch in aiming at completeness could not do this, yet he has coped most successfully with obsolescence of algal literature.

The foreword offers a short outline of the ecology and distribution of seaweeds; it is very brief, and quite justly so, since these volumes do not attempt to cover the whole biology of the algae. In some respects the material here does not measure up to the high standard of the rest of the volume. The folding maps at the rear are particularly inconvenient; broken up into smaller units and used as text-figures in the appropriate place they would have been much more effective. The data on which the distribution is based seem in some cases to have been incomplete; for instance, the southern boundary for the Agareae on the American coast is set on Labrador, though these plants are well known to occur in northern Massachusetts, and for the Laminariales in general it is set on Nova Scotia, though these plants are common off southern Massachusetts, and are represented as far south as New Jersey.

The morphology and reproduction of the Phaeophyceae are handled together group by group, with a special section correlating our information on life histories. The works of Sauvageau, Svedelius and Kylin have contributed most to the expansion of the account over the earlier compilations. The morphological features are fully presented, and the importance of the primitive heterostichous state is developed. Returning the emphasis to the vegetative structure rather than the state of reproductive differentiation, in arranging the orders an interesting change of emphasis is seen. The Punctariales and Dictyosiphonales are not recognized as distinct, these forms being held as climax types in the ectocarpalean series. The Desmarestiales and Laminariales are moved forward to follow the Cutleriales in spite of their contrasted generations, because of the generalized nature of the sporophyte growing region and the lack of specialized sporangium-bearing structures. The Sphacelariales are immediately followed by the Dictyotales, both being orders with prominent apical cell growth, and rather logically are directly followed by the Fucales with modified apical growth.

In the organization of the chapters on the Rhodophyceae no such striking position is assumed. The author accepts the customary division into Bangioideae and Florideae as based on wide divergences in structure and spore formation. In the first subclass the most distinctive move is to expand the Porphyridiaceae to include the filamentous genera *Asterocytes* and *Goniotrichum* because of the similarities in cell structure and simple reproduction. The families of the Florideae are first considered from the standpoint of general structure, which calls for elaborate detail regarding a great many genera. The heterostichous habit of growth is considered fundamental to both the uniaxial and multiaxial types, just as in the Phaeophyceae, and as lost only in the Ceramiales. Except for developmental details this is essentially familiar material. Short sections on symbiosis and other special ecological types, special cell contents and the like complete this part. Reproduction is then treated in a separate review of the families, where it has been possible to concentrate on representative types of each family, for relatively few species have been thoroughly analysed. A large proportion of this material is recent, based on the work of Svedelius, Kylin and other contemporary investigators; the general classification adopted by Kylin is followed, except that the Dasyaceae are considered the climax family.

The Myxophyceae are chiefly treated in general sections and the systematic treatment is more brief, favoured by the comparatively low degree of plant organization. The result is a very usable section, perhaps rather more attractive to the reader than the very detailed treatment of the Rhodophyceae, though far more thorough than anything elsewhere available.

The two volumes of this work by Fritsch are of about equal thickness. The second volume is about 150 pages longer, but by the use of slightly thinner paper and cover boards this has been overcome. The quality of the paper is commendable under war-time circumstances; one hopes that it is actually durable, because the book should remain in active service for decades. Its slightly grey, uneven colour betrays the difficulties under which it was produced. The 336 groups of pictures give a wealth of illustration vastly greater than has been attempted in a work of this kind before. The great preponderance have not previously been used in a text-book and are from the most recent research publications. Reproduction of the line drawings is very good; the half-tone cuts have been exceedingly carefully prepared by the engraver, but the texture of the paper has militated against results as satisfactory as were obtained in the first volume. The cloth, boards and binding seem too light for a work of this bulk and potential length of service.

In summary, we have now for the first time in English a comprehensive account of algal morphology, including reproduction, adequately related to physiology, ecology and suggested evolutionary trends, in a form so excellent and complete that it has no competitor in any language. Its enduring utility will but emphasize the great accomplishment which it presents.

WM. RANDOLPH TAYLOR

Trees and Toadstools. By M. C. RAYNER. $5\frac{1}{4} \times 8\frac{1}{2}$ in. Pp. 72 with 18 plates. London: Faber and Faber. 1945. 6s.

Not long ago Dr Rayner's striking and provocative research work upon the mycorrhizal relationships of trees was reviewed in this journal (vol. 43, p. 179). The small but attractive book now dealt with is an exposition of this field of natural sciences in terms suitable for the intelligent layman and unspecialized botanist. It explains simply and effectively the characteristics of the higher fungi, their morphology and nutritional habits, and then fluently sets out the exciting story of Frank's discovery of the mycorrhizal habit, and the expansion of research by authorities such as Melin, who have identified as mycorrhiza formers so many of the common woodland toadstools. The concept of symbiosis as originally put forward by Du Bary, and as later restricted, is explained and made the basis for a consideration of the physiological relationships of the 'partners' in mycorrhizal trees. Dr Rayner faithfully quotes opinion that the association 'is to be regarded as an example of controlled parasitic attack and has no mutualistic significance', but makes no bones about the fact that she disagrees with this view.

There is both advantage and disadvantage in writing popularly upon a field of scientific controversy, and here both are disclosed. The advantage is that by the necessary simplification the author's outlook is more genuinely and easily displayed: the disadvantage that the critical structure of argument and experiment is here out of place, and must be omitted, although thereby the means of reaching decisive conclusion is excluded. Dr Rayner evidently gives great weight to the fact that the healthier a tree the more profuse are its mycorrhiza, and to such results of experience as the nursery practice of infecting seedling tree beds in non-woodland soils with mycorrhizal fungi. She is assured that 'there is conclusive experimental evidence that normal healthy and vigorous growth of the host-trees follows upon and is directly related with the free development of mycorrhizas'. One cannot, however, help the reflexion that all healthy trees must in any case show a free development of rootlets, and that the case for the relationship being beneficial to the tree rests upon the controlled experiments of growth of inoculated and fungus-free trees, experiments here mentioned only briefly and represented perhaps too persuasively by three excellent selected photographs.

Dr Rayner rightly stresses the need for recognition of the intricacy of conditions in the soil, and recommends attention to soil ecology.

Eighteen very attractive and informative plates are a feature of this book, and with the easily readable text will provide a means of introducing many to a field of scientific study where, thanks to the vigour of scientists like Dr Rayner, discoveries are still being made, and healthy controversy still prevails.

H. GODWIN

SWISS CONTRIBUTIONS TO QUATERNARY HISTORY

By V. M. CONWAY

(i) *Die Waldgeschichte des südlichen Tessin seit dem Rückzug der Gletscher.* By W. LÜDI; and *Sublakustre alluviale Torfe u. humose Sande im Luganersee.* By A. JEANNET u. W. LÜDI. In *Bericht über das Geobot. Forschungsinst. Rübel in Zürich.* 1943.

The work of main weight and interest in this volume is contributed by Dr Lüdi in the first article, on the post-glacial forest history of southern Tessin. It is supplemented by the second article which affords pollen analytical data from peat beds beside the Lake of Lugano. These peat beds lie at about 266 m.; of the other sites investigated, five lie at altitudes of from 300 to 400 m., and one at about 600 m. They are situated in valleys all within 15 miles of the town of Lugano. The pollen-yielding strata are mainly lake deposits, though in most of the sites the upper layers are formed of peat.

Taken together, these pollen diagrams give a picture of four main phases in the district of southern Tessin; they may be referred to for convenience as I, Treeless; II, *Pinus-Betula*; III, *Quercus-Alnus*; IV, *Castanea*. That the first phase was treeless is deducible from the high non-tree-pollen percentage; the tree pollen recorded from these lowest horizons is attributed to transport from the more distant Lombardy plain, where forest development could presumably start some time before the retreating glaciers left bare the mountain valleys further north. *Pinus* (probably

P. sylvestris) is the most abundant pollen in this phase, but lesser quantities of quite a variety of other trees also occur, *Alnus* (probably *A. viridis* and *A. incana*) and *Abies* showing values up to 30% in places, with *Betula, Quercus, Fagus, Corylus* in smaller quantity, and scattered grains of *Castanea* and *Ostrya*. At one of the sites (Muzzano) this phase shows a division into three, the middle stage indicating a recession of warmth-loving trees and increase of *Betula*. The author tentatively interprets this as evidence of an adverse fluctuation in climate, but this interpretation must probably await confirmatory evidence from a wider area.

The second or *Pinus-Betula* phase shows a consistent and intriguing feature in that the general dominance of *Pinus* (now probably *P. mugo*) is interrupted temporarily by a period of birch dominance. The author discusses this primarily in terms of climatic fluctuation, though without reaching any definite conclusion. He also deals carefully with the whole of the pine-birch phase as an indication of climatic conditions and changes, but interpretation is made harder by the evidence that the Tessin area itself was becoming forest-clad in the course of this phase. It is clear from the pollen diagrams that the *Betula* interpolation is correlated with the rather sudden and large change in non-tree/tree pollen ratio and in tree and shrub pollen frequency which must indicate the time of establishment of woodland at the site itself. Without data as to the exact species of *Betula* involved, and without intimate knowledge of the characteristic successions of the area, one cannot venture to offer an alternative interpretation of the *Betula* maximum, but one may perhaps at least raise the question as to whether the pollen spectra at this level may not reflect successional change rather than climatic fluctuation.

Phase III is characterized by high *Alnus* values, with *Quercus* usually second in importance, while *Abies* and *Fagus* may both rise to values round 20% at times. In general, the variety is greater than in Phase II and gives the impression of 'warmth-loving' forests, an impression usually associated with the descriptive name Eichenmischwald. The Tessin diagrams, however, show *Corylus* as unimportant except for a small and interesting maximum just at the beginning of the phase, while *Ulmus* and *Tilia* nowhere leave more than traces of their existence. It is noteworthy that at the Lugano sites, which give pollen spectra attributable on other grounds to this phase, *Abies* is the most abundant pollen, not *Quercus* or *Alnus*. *Fagus*, again, is interesting because it is more frequent and constant in this phase than in the others, though even here it never reaches really high values.

The last or *Castanea* phase gives us, as the name suggests, pollen spectra which are unfamiliar to north-west Europe, since, as Rikli* has said, *Castanea* is to us the 'symbol of the south'. The *Castanea* pollen curves do not remain constantly dominant but fluctuate rather wildly, alternating in one locality with *Alnus*, in another with *Ostrya*, and in a third with *Juglans*, though in this case the dominance of *Juglans* is fleeting. The high pollen percentages of *Juglans*, a tree not considered native of this part of Europe but widely cultivated, and of *Ostrya* and *Castanea*, both often used for various human purposes if not actually planted, must raise the question of widespread human interference with the natural forest cover. The evidence is against these trees having been introduced for the first time by man in this period, since their pollen is present in small quantities throughout the profiles. The author leans to the view, however, that their predominance over the other forest trees may be at least in part an effect of human silviculture and attributes the fluctuations in the pollen curves to the inconstancy of human enterprise.

It is of some interest to compare this picture from Tessin, on the southern face of the Alps, with results of similar scope from the northern face, and as examples of the latter we may take Härri's work on the Wauwilermoos,† about 20 miles north-west of Lucerne (altitude 500 m.), and Welten's on the Faulenseemoos,‡ by the Lake of Thun (altitude 560 m.). As one would expect from the work of Von Post on correlations over a far wider area, there are broad similarities on both sides of the Alps. Thus an initial treeless phase is followed by a *Pinus-Betula* phase and this by an 'oak and other hardwood phase'.

The treeless and the pine-birch phases both show subdivisions in all three districts, and all three authors put forward tentative suggestions as to how these minor fluctuations might be interpreted in terms of fluctuations in climatic 'favourability'. It is not easy, and it would be very rash on the basis of the published diagrams alone, to correlate these subdivisions, but it seems likely that such a correlation may be possible in the future.

* Rikli, M., *Das Pflanzenkleid der Mittelmeerländer*.

† Härri, H., 'Stratigraphie u. Waldgeschichte des Wauwilermooses', *Veröff. d. Geobot. Inst. Rübel in Zürich*, 17, 1940.

‡ Welten, Max, 'Pollenanalytische, stratigraphische, u. geochronologische Untersuchungen aus dem Faulenseemoos bei Speiz', *Veröff. Geobot. Forsch. Inst. Rübel in Zürich*, 21, 1944. (This publication is reviewed on p. 241.)

Härri's data show that the beginning of the 'oak' phase is correlated with a Mesolithic horizon, the end with a Neolithic, and this holds good roughly speaking for the Tessin district too, though the correlations here are more tentative. There seems then no reason to doubt the homology of the oak phases on both sides of the Alps in spite of differences of expression, especially with regard to *Corylus*, *Tilia* and *Ulmus* (all unimportant in Tessin) and of possible doubt as to identity of the actual species.

But when we look at the latest stages we find that although in all three districts there is a change in the pollen picture after the oak stage, the scene which follows it in Tessin is widely different from those given by the Wauwil and Faulensee regions, which, though they may not agree with one another in detail, both show *Abies* and *Fagus* as the main features of the landscape. Tessin, on the contrary, does not give values of these genera which are any higher than those in the oak phase, in spite of the fact that *Fagus* still forms extensive woodlands up to the tree limit at the present day in Tessin. Three possibilities suggest themselves in this connexion: first, the Tessin sites and the northern sites may not be situated in the same position relative to the altitudinal zonation of forest types, and the Tessin history should therefore be compared with areas on the north face which lie farther from the mountain centre. Secondly, the same general climatic drift may have affected both faces of the Alps but called out a different vegetational response, in other words, *Castanea-Juglans* in Tessin is the homologue of *Fagus-Abies* in Bern and Lucerne. Thirdly, such a climatic change may not have been largely if at all effective on the south face, which might therefore still carry forests of the oak-phase type were it not that *Castanea* and *Juglans* have become exaggerated through human influence. All three ideas may contain partial aspects of the true interpretation, and the third point in particular must be partly valid if we accept Lüdi's interpretation of phase IV as showing marked influences of human silviculture, in the sense that whatever the natural climax which would be appropriate to the phase IV type of climate, the actual forest composition is a modification.

Here we have a point of comparison and at the same time an interesting difference between the Tessin results and those at Wauwil. In the latter case, Härri in his summarizing diagram indicates tentatively that A.D. 1000 might be approximately the time at which human influence on the forest cover became sufficiently great to show its impress by a change in the relative proportions of the forest trees. The period later than this he calls 'Zeit der letzten Rodungen und der Waldkulturen'. He does not of course suggest that this is the first date at which his area was extensively inhabited, quite the reverse; but it is not until this level that any marked effect can be seen in the tree-pollen curves themselves. Yet in the Tessin diagrams the rapid rise of *Castanea* to high values is shown at a far earlier date, that is, immediately after the oak phase and hence (transferring Härri's dating to the southern side of the Alps) round about 2000 B.C. Such a wide difference in date of the beginning of large-scale human effects on forest cover might well be expected from our knowledge of the human history of Europe, with its early development of complex civilizations in the Mediterranean basin while outlying races were still far more primitive.

It is impossible within the space of a review to touch on the many other points which arise both in the data and the discussion of Dr Lüdi's highly interesting paper, and one must hope that before very long these results may be extended and clarified by other investigations in regions along the southern slopes of the Alps, regions which, except in the case of Tessin, do not for the most part lie within the borders of Switzerland.

(ii) *Pollenanalytische, stratigraphische und geochronologische Untersuchungen aus dem Faulenseemoos bei Spiez*. By MAX WELTEN. 9 × 6½ in. Pp. 201, with 30 text-figures. *Veröff. d. Geobot. Inst. Rübel in Zürich*, 21. Heft. Bern: Hans Huber, 1944. Price Swiss Fr. 12.50.

It is hard to exaggerate the value of this account of the lake deposits of the Faulensee. Not only is the material exceptionally favourable, but it has been examined with an admirable thoroughness and variety of method. Of the many striking results obtained, by far the most outstanding is the establishment of a time-scale for the whole post-glacial period in this region of the Swiss Alps.

The deposits were formed in a small shallow lake lying at a height of 590 m., close by the Lake of Thun. The small lake originated from the blocking of a drainage channel by the moraines of the Aar valley glacier, and it has been possible to demonstrate a sequence of forest history which covers the time since the ice left the area until the present day. This sequence agrees with the already established scheme of forest phases which has emerged from the pollen-analytical work hitherto

carried out in this part of Switzerland. The Faulensee sequence, with its time-scale, may be summarized as follows:

c. 8000 B.C. Retreat of glacier. Suggested correlation with Salpausselkä stages II and III in northern Europe, and the Thun and Jaberg phases of Alpine Glaciology.

Until 7550 B.C. *Salix* period. Section 1. With *Pinus.*
7550–7150 B.C. *Salix* period. Section 2. With *Helianthemum.*
7150–6750 B.C. *Salix* period. Section 3. With *Betula.*
6750–6630 B.C. *Hippophaë* phase.
6630–6350 B.C. *Betula* period.

— Suggested as the equivalent of the Finiglacial period of northern Europe.

6350–6000 B.C. ⎫
6000–5400 B.C. ⎬ *Pinus* period. ⎰ *Betula + Pinus.*
5400–5050 B.C. ⎭   ⎱ Pure *Pinus.*
                                   Secondary *Betula* increase.
5050–3200 B.C. EMW period (*Ulmus* predominant, with high values of *Corylus* in the first half).
3200–2350 B.C. First *Fagus* period.
2350–1800 B.C. *Abies* period.
1800 B.C.–*c.* A.D. 1300. Period of alternating *Fagus* dominance with 'Mixed *Fagus*' (BMW).
c. A.D. 1300–A.D. 1920. BMW period, with *Picea* mainly pre-eminent, and *Juglans* present.

The author treats the period 1800 B.C.–A.D. 1300 in much more detail than is here suggested. We will return to some discussion of the period later. Meanwhile, however, it may be worth describing some features of the profile from which the nature of the period is mainly deduced, to give an illustration of the wealth of data provided, and of the amount of work involved. This profile is 12 m. deep, of which the lowest metre only was occupied by deposits of the EMW period. Pollen analyses were made at intervals of 5 cm. for the lowest 4 m. and of 10 cm. for the overlying 8 m. Moreover, each sample was analysed into organic, chalk, and clay fractions.

Investigations of other kinds were made in addition in the profiles which were worked out later than this one and which cover the earlier phases. It is from these that the evidence for the time-scale is largely derived, for it is these which were found to show a small-scale lamination of the deposits, which strongly suggested an annual periodicity. The further evidence concerning these layers leaves no doubt that they do in fact correspond to the 'varves' on which De Geer's Scandinavian geochronology is based. Moreover, they are almost perfectly preserved in a single profile over the whole of the time from the beginning of the second section of the *Salix* period to the end of the first *Fagus* period. A second profile overlaps the first for the length of the first *Fagus* period (agreeing closely in the number of annual layers found in it) and then gives a clear record for the next 1700 years and a rather less reliable record for the succeeding 800 years. Including this latter 800 years, this gives a period of 8000 years over which the lengths of the phases of the pollen diagrams can be measured to the nearest 50 years. The author claims that the errors over the whole pre-Christian era are of an order not exceeding 200 years. Unfortunately, the laminae are missing or almost missing in the profile which comes up to the present day, so that a difficulty arises in placing the time-scale in relation to 0 A.D. This difficulty is met by an extrapolation based on the relation between sedimentation rate and depth, though it might perhaps be doubted whether the assumptions involved are very solidly based. However, the EMW, first *Fagus*, and *Abies* periods in the Alps are already linked with known archaeological horizons, and hence with a fairly secure dating, and the extrapolation brings these periods in the Faulensee to the right dating on this basis. Other supports are brought in, and in general, it seems possible to accept the first firm date of the scheme, 7550 B.C., as substantially correct.

Such a clearly established time-scale is obviously of the greatest importance in any attempt to make parallels between climatic and vegetational fluctuations in widely separated regions. So far only Scandinavia has possessed a time-scale of this sort, but data should soon be available from the British Isles, and then it should be possible to sort out some of the vexed questions concerning the varying effects of a given general climatic shift in different latitudes and at different distances from oceanic influences. Again, the possibility of close dating within periods of less than 1000 years throws most welcome light on the ecological problems which arise in considering the transition conditions between one type of forest climax and another. Thus the short duration—120 years— of the *Hippophaë* stage make it plausible to regard this as being a temporary colonization of a non-woodland vegetation by a fast spreading bush, which is soon to give way to the climax woodland (*Betula*) appropriate to the new climate.

Another most laborious set of measurements has been applied to the separation of species within a genus on the basis of pollen-grain size. The two genera concerned are *Betula* and *Pinus*, and statistical data were collected from the birch and pine periods. In the case of *Betula* there is good evidence for deciding whether at any time the pollen is predominantly that of *Betula nana*,

B. verrucosa, or *B. pubescens*. A remarkably clear and interesting picture is given by the diagram which shows the size-frequency curves for more than thirty samples from the *Salix* period to the beginning of the EMW period. Preponderant *Betula nana* in the *Salix* period is succeeded by *Betula pubescens* early in the birch period. Then the more exacting *B. verrucosa* is continuously the most abundant until the central pure pine phase of the *Pinus* period and here there is a quite definite and maintained swing-over to *Betula pubescens*. *B. verrucosa* then reasserts itself in the secondary birch increase.

The measurements on pine pollen give less satisfactory indications, especially as the possibility of separating *Pinus montana* and *P. sylvestris* does not seem obvious from the data which are given. *P. cembra* at any rate does not appear to be present. Further, if we accept the author's interpretation that a greater number of smaller grains indicates *P. sylvestris*, of larger grains, *P. montana*, the size-frequency curves suggest that the chief pine of the pure pine phase is *P. montana*, whereas *P. sylvestris* has been prominent both before and after. Observations on the morphological characters of the grains support the interpretation.

This is taken to indicate a 'Klimarückschlag', and while the evidence on the basis of pine pollen alone is decidedly slender, there are other lines of evidence which make it seem at least plausible. One is the already mentioned replacement of *Betula verrucosa* by *B. pubescens*; another is a quite definite lowering of the absolute tree-pollen frequency; a third is a slight increase in the proportion of alluvium (Einschwemmung) relative to lake marl (Seekreide), which may indicate increased precipitation, and a decrease in the organic content of the sediments. It is suggested that this unfavourable period is an expression of a 'Schlussvereisung' occurring at higher altitudes, possibly the Daun or the Gschnitz stage. The dating of this suggested climatic regression—6000–5400 B.C. —makes it hard to find anything to compare with it in the record of events in north-west Europe, though this is no argument against the hypothesis, which must be proved or disproved on the internal evidence for that region of the Alps.

Whether or not this interpretation of the pine phase turns out to be justified, it seems quite clear that the preceding *Betula* period cannot be taken to indicate a climatic retrogression, as has been suggested by Härri, but indicates rather the onset of true forest vegetation in response to climatic improvement. The strongest argument for this view comes from the curves of absolute pollen frequency. They are based for the most part on the pollen densities on the prepared slides, and the agreement in behaviour from one profile to another quite justifies this method of comparison. Full confirmation of the conclusions is derived, moreover, from the investigation in one of the profiles of the total pollen content of a known volume covering a known number of years, and thus a truly 'absolute' value for the pollen rain per cm.² per annum is achieved. Some of the figures for these values are worth quoting:

	grains/cm.²/year
Last *Salix* maximum	29
Early *Hippophaë* phase	119
Maximum *Hippophaë* phase	163
First *Betula* period sample	630
Betula maximum	970
Highest value in the *Betula-Pinus* phase	4340
Average value in the pure *Pinus* phase	c. 1700
Maximum value during secondary *Betula* increase	8300

As the author points out, some of the changes in density of the pollen rain are very sudden; for instance, it may be multiplied three or more times in the course of 50 years, so that there is a strong probability that the first response to a climatic change is a change in the pollen production by the trees that are present, and only more slowly is there a change in the actual number of trees, or in the type of tree.

The absolute curves for grasses and herbs also give some valuable information. While this type of pollen, when given in percentage of tree pollen, appears important only in the *Salix* period, the absolute amounts at that time are negligible, and herbs, grasses and ferns all show their maximum development in the later stages, thus supporting the idea of a radical improvement in climate at the end of the *Salix* period.

Perhaps the most fascinating application of this approach is the treatment of individual annual laminae. Samples were taken from the material of the brown (mainly organic) and white (chalk) layers whose alternations make up the visible periodicity. Not only that, but two or sometimes three samples were taken at different levels within each of these bands. When it is realized that the layers were of the order of 1 mm. thick, the skill involved becomes apparent! The curves for absolute pollen numbers for the separate species show maxima in positions which make it clear that the

brown layer represents autumn, winter, spring and early summer, the white layer mid- and late summer.

The data concerning the clay, chalk and organic percentages in the samples do not lend themselves to direct and simple interpretations, and it would be a long task to review either the data or the author's very stimulating discussion of them. To select a few points for comment, however, we may mention first of all some fairly clear features of the curve for percentage organic matter. This shows general values of 10 % or under, though with a rising tendency, until the *Betula-Pinus* phase, the end of which shows a maximum. Lower values in the pure pine phase are followed by a sudden rise at the beginning of the second *Betula* increase to a level averaging 18 % which is maintained, though with large fluctuations, until the surface layers, i.e. until the present century, except for a small number of sudden large maxima (40 % or over). Of the latter, those falling after the EMW period are correlated with Granlund's recurrence horizons. The Grenz horizon thus finds itself placed round about 600–400 B.C. on the Faulensee time-scale, which renders the interpretation plausible. It is further supported by the grass-pollen curve which shows sudden peak values immediately following the supposed Grenz level, and then falls off gradually.

The rise in organic matter at the beginning of the secondary birch increase is interpreted to mean that a major climatic change took place at this level and is reflected immediately in the sediments, but only much more slowly by the replacement of *Pinus* by EMW. The increasing birch (mainly *Betula verrucosa*) is therefore seen as the forerunner of the EMW—a transitional phase like the *Hippophaë*, and not a stable type of vegetation. This would place the main climatic change at *c.* 5400 B.C. which of course strongly suggests the north European Boreal-Atlantic transition, though such a correlation would make it hard to find in the Swiss data the equivalent of the warmth increase which clearly preceded the Boreal-Atlantic transition in northern Europe—hard, at any rate, if we accept the Swiss pine period as one of relatively adverse climate.

The percentages of clay and chalk in the samples are converted into absolute yearly thicknesses of lake marl and alluvium on the assumption that alluvium always contains a certain amount of chalk; 40 % is assumed for the lower samples, 20 % for the higher ones. A scatter diagram has been constructed with alluvium as abscissa and lake marl as ordinate, plotting a large number of samples each in their appropriate positions. One may not like the assumptions made in the calculations, and one may not be prepared wholly to accept the conclusions as to climatic types which the author reaches on the basis that more alluvium indicates greater precipitation, more lake marl a higher temperature. Nevertheless, the scatter diagram shows that this treatment of the data may bring out facts of much significance, because the samples within any one of the forest phases are grouped together in a very striking way, with very little overlap between the different groups. It appears from the diagram that lake marl and alluvium are inversely correlated; that the *Salix* period shows the most alluvium and the least lake marl; that the EMW period shows least alluvium values on the whole, especially during the first half; that the *Betula* period shows more lake marl than the pine period, and so on. The results lead the author to conclude, among other points, that the EMW was the driest and warmest, the first beech period the wettest and warmest of the periods covered by the profile on which these results were obtained.

Finally, a little must be said about the post-EMW periods. Here the interpretations of the pollen diagrams have to be taken with more reserve, and indeed they are put forward somewhat tentatively. The difficulties are due partly to the absence of varves in the later stages, partly to the scarcity of other comparably full diagrams for the region, partly to the strong probability of human influence on the forest cover. Following the *Abies* period, the pollen curves show three mixed beech periods (very mixed, but with *Alnus* and *Corylus* often prominent), alternating with three beech periods. The earliest of the latter includes the suggested 'Grenz' layer; the last is followed by what is called the fourth mixed beech period from about A.D. 1300 onwards, but which might well be called by some other name, since *Picea* is the most frequently predominating pollen, and *Juglans* is constantly present, showing that over this period human influence is not merely probable but certain. It may also be of importance at earlier times, since it is known that sites near the Faulensee have been inhabited since Bronze age times. Hence while it is possible to suggest climatic causes for the fluctuations in beech dominance, as, indeed, the author has done, it would seem that further evidence is necessary before they can be fully understood.

Naturally, it is likely that a number of the minor points arising in the two hundred pages of this richly suggestive treatise should be open to question and maybe in some cases to criticism, either from pollen analysts, ecologists, limnologists, glaciologists, meteorologists or archaeologists. But all these groups, and no doubt others besides, will find here an abundance of interesting matter—a tribute to the many-sidedness of the work and to its fundamental importance in the study of post-glacial history.

ADDRESS LIST OF BOTANISTS

IN COUNTRIES FORMERLY OCCUPIED BY THE ENEMY

NOVEMBER 1945

The Editors of the *New Phytologist* publish this list to assist the re-establishment of communication with scientific colleagues. It is very incomplete and additions will be welcomed.

DENMARK

ANDERSEN, Alfred, Mag. scient. Danmarks geologiske Undersøgelser, Charlottenlund, Copenhagen. (Pollen statistics.)

ANDERSEN, Svend, Director. Kastanievej 5, Holte. (Floristics.)

BJØRNEKÆR, K., Teacher. Ved Klosteret 25, Copenhagen. (Fungi.)

BORNEBUSCH, C. H., Dr. phil., Forstander. Statens forstlige Forsøgsvæsen, Springforbi. (Forestry. Ecology of woodlands.)

BUCHWALD, N. F., Professor. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Fungi. Phytopathology.)

BÖCHER, Tyge W., Dr. phil. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Phytogeography. Cytology.)

BØRGESEN, F., Dr. phil. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Marine Algae.)

CHRISTENSEN, Tyge, Stud. mag. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Bryophytes. Green algae.)

CHRISTIANSEN, M. Skytte, Stud. mag. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Lichens.)

CLAUSEN, Eva, Cand. mag. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Hepaticae.)

FJERDINGSTAD, Ejner, Head clerk. Vangeleddet 51, Lyngby. (Phytoplankton.)

FLOTO, E., Branch-chief. Universitets botaniske Have, Ø. Farimagsgade 2 B, Copenhagen. (Horticulture.)

FRANDSEN, N. O., Mag. agro. Toftehøj pr. Maaløv. (Plant breeding. Genetics.)

GABRIELSEN, E. K., Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Plant physiology.)

GALLØE, O., Lector, Dr. phil. Nybrovej 176, Lyngby. (Lichens.)

GELTING, Paul E., Dr. phil. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Lichens. Arctic vegetation.)

GRAM, Ernst, Direktor. Statens plantepatologiske Forsøg, Lyngby. (Plant pathology.)

GRAM, Kai, Professor, Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Taxonomy. Phytogeography.)

GRØN, A. Howard, Dr. phil., Professor. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Forestry.)

GRÖNTVED, Johs., Bibliotekar. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Arctic vegetation.)

GRØNTVED, Jul., Mag. scient. Plankton-Laboratoriet, Charlottenlund Slot, Copenhagen. (Phytoplankton.)

GRØNTVED, P., Konsulent. Farimagsvej 8, Næstved. (Agricultural botany.)

GUDJONSSON, G., Mag. scient. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Cytology.)

HAGERUP, O., Museumsinspektør, Dr. phil. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Morphology. Cytology. Bryophytes.)

HANSEN, H. Mølholm, Dr. phil. Universitetets botaniske Museum, Gothersgade 140, Copenhagen. (Plant geography. Phytopaleontology. Lichens.)

HARMSEN, L., Cand. mag. Brødhøj 10, Gentofte. (Bryophytes. Cytology.)

HERRING, P., Mag. art. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Rosa.)

HERTZ, V., Physician. Skjoldsgade 11, Copenhagen. (Fungi.)

HESSELBO, Aug., Cand. pharm. Bellmans Plads 22, Copenhagen. (Bryophytes.)

IVERSEN, Johs., Statsgeolog. Danmarks geologiske Undersøgelser, Charlottenlund. (Pollen statistics. Ecology.)

JENSEN, P. Boysen, Professor, Dr. phil. Universitetets plantefysiologiske Laboratorium, Gothersgade 140, Copenhagen. (Plant physiology.)

JENSEN, Hjalmar, Professor. Gersonsvej 55, Hellerup. (Microbiology.)

JENSEN, H. Nilaus, Chief gardener. Universitets botaniske Have, Ø. Farimagsgade 2A, Copenhagen. (Botanical Gardens.)

JENSEN, Vald., Director. Vilvorde, Charlottenlund. (Horticulture.)

JESSEN, Knud, Professor, Dr. phil. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Pollen statistics. Plant geography. Culture-botany.)

JOHANSEN, Gudrun, Cand. hort. Statens plantepatologiske Forsøg, Lyngby. (Mycology.)

JONASSEN, H.. Cand. mag. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Pollen statistics.)

JUEL, Inger, Mag. scient. Universitetets plantefysiologiske Laboratorium, Gothersgade 140, Copenhagen. (Plant physiology.)

JØRGENSEN, C. A., Professor, Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Mycology. Genetics. Cytology.)

JØRGENSEN, H., Cand. mag. Ribe. (Pollen and pollination.)

KJÆR, Arne, Mag. scient. Schæffergaardsvej 10, Gentofte. (Plant physiology. Seeds.)

KLINGE, Axel B., Confidential clerk. Gl. Viborgvej 2, Hornbæk, Randers. (Fungi.)

KØIE, Mogens, Mag. scient. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Ecology. Bryophytes.)

LANGE, Johan, Cand. hort. Næsbyholmvej 23, Brønshøj, Copenhagen. (Horticulture. Botanical etymology.)

LANGE, Morten, Cand. mag. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Fungi.)

LARSEN, C. Muhle, Forstkandidat. Arboretet, Hørsholm. (Tree breeding.)

LARSEN, Poul, Dr. phil. Universitets plantefysiologiske Laboratorium, Gothersgade 140, Copenhagen. (Plant physiology.)

LARSEN, C. Syrach, Director, Dr. agro. Arboretet, Hørsholm. (Tree breeding. Cytology.)

LUND, Aage, Mag. scient. V. E. Gamborgsvej 10, Copenhagen. (Fungi. Microbiology.)

LUND, Mogens, Lektor. Ulrikkenborg Allé 6, Lyngby. (Lichens.)

LUND, Søren, Mag. scient. Havundersøgelserne, Charlottenlund Slot, Copenhagen. (Marine Algae.)

MATHIESEN, Fr. J., Professor. Danmarks farmaceutiske Højskole, Universitetsparken 2, Copenhagen. (Plant anatomy. Phytopaleontology.)

MIKKELSEN, Valdemar, Cand. mag. Danmarks farmaceutiske Højskole, Universitetsparken 2, Copenhagen. (Pollen statistics.)

MUNK, Anders, Stud. mag. Universitetets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Fungi.)

MÜLLER, D., Professor, Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Plant physiology.)

MØLLER, Carl Mar., Professor, Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Forestry.)

MØLLER, F. H., Teacher. Vesterskovvej 66, Nykøbing F. (Fungi.)

NEERGAARD, Paul, Research-chief, Dr. agro. Gothersgade 158, Copenhagen. (Fungi. Plant pathology.)

NIELSEN, E. Steemann, Professor, Dr. phil. Danmarks farmaceutiske Højskole, Universitetsparken 2, Copenhagen. (Phytoplankton. Plant physiology.)

NIELSEN, Niels, Dr. phil. Carlsberg Laboratoriet, Valby, Copenhagen. (Plant physiology.)

NYGAARD, G., Cand. mag. Søndre Landevej 10, Sønderborg. (Phytoplankton.)

OLSEN, Carsten, Dr. phil. Carlsberg Laboratoriet, Valby, Copenhagen. (Ecology. Plant physiology.)

OLSEN, Sigurd, Assistant. Hovedgaden 64, Lyngby. (Limnology.)

ORLA-JENSEN, S., Professor, Dr. phil. Kastelsvej 1, Copenhagen. (Bacteriology.)

PAULSEN, Ove, Professor, Dr. phil. Brogaardsvænge 3, Gentofte. (Phytogeography. Phytoplankton.)

PEDERSEN, Anton, Professor. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Horticulture.)

PEDERSEN, Axel, Professor. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Agricultural botany.)

PETERSEN, J. Boye, Lektor. Dr. phil. Universitets botaniske Museum, Gothersgade 130, Copenhagen. (Algae. Microbiology.)

PETERSEN, Erik J., Lektor, Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Microbiology.)

PETERSEN, Henning E., Docent, Dr. phil. Universitets planteanatomiske Laboratorium, Gothersgade 140, Copenhagen. (Marine algae. Mycology.)

PORSILD, M. P., Director, Mag. scient. Godhavn, Disco, Greenland. (Arctic plants.)

RASMUSSEN, R., Teacher. Thorshavn, The Faroes. (Floristics.)

ROMOSE, V., Dr. phil. Kirketorvet, Slangerup. (Bryophytes. Plant physiology.)

SEIDENFADEN, G., Cand. polit. Stormgade 6, Copenhagen. (Arctic plants.)

SKOVSTED, Aage, Dr. phil. Carlsberg Laboratorium, Valby, Copenhagen. (Cytology. Genetics.)

STAHL, Chr., Director. Thorvaldsensvej 57, Copenhagen. (Seeds. Germination.)

SØRENSEN, Henning. Balders Plads 2, Copenhagen. (Floristics.)

SØRENSEN, Thorvald, Dr. phil. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Arctic vegetation. Genetics.)

TRESCHOW, C., Dr. agro. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Fungi. Plant physiology.)

TROELS-SMITH, Jørgen, Mag. scient. Nationalmuseet, Copenhagen. (Pollen statistics.)

VAHL, M., Professor, Dr. phil. Skrænten 5, Gentofte. (Plant geography.)

WANSCHER, J. H., Mag. scient. Landbohøjskolen, Rolighedsvej 23, Copenhagen. (Cytology. Genetics.)

WEBER, Anna, Cand. hort. Statens plantepatologiske Forsøg, Lyngby. (Phytopathology.)

WESTERGAARD, Mogens, Dr. phil. Landbohøjskolens Arvelighedslaboratorium, Rolighedsvej 23, Copenhagen. (Cytology. Genetics.)

WIINSTEDT, K., Conservator. Universitetets botaniske Museum, Gothersgade 130, Copenhagen. (Floristics.)

WINGE, Øjvind, Professor, Dr. phil. Carlsberg Laboratorium, Valby, Copenhagen. (Genetics. Cytology. Fungi.)

ØSTERGAARD, Jend, Cand. hort. Aaløkkevej 3 B, Copenhagen. (Horticulture.)

HOLLAND

BEYERINCK, Dr W. A. Wijster Drenthe.

ESHUIS, J. H. Leusden, B 20 a (post Amersfoort).

FLORSCHÜTZ, F. Enkstraat 37, Velp.

JONKER, Dr F. P. Nassaustraat 30, Utrecht.

MULLER, J. Diedenweg 39, Wageningen.

POLAK, Dr B. Hortus Botanicus, Amsterdam.

PULLE, Dr A. Javalaan 5, Baarn.

VAN SOMEREN, Miss A. M. H. Dennenweg 3, Velp (9).

WASSINK, Dr. E. C. Hobbemastraat 2 bis, Utrecht.

NORWAY

ÅLVIK, Dr. Ås University.

DAHL, E. Oslo University.

FAEGRI, Dr K. Botany Department, Bergen University.

HOEG, Dr. Trondhjem University.

HYGEN, G. Oslo University.

JØRSTAD, Dr. Statens plantepatologiske Institutt, Oslo.

NORDHAJEN, Prof. R. Bergen University.

PRINTZ, Prof. Oslo University.

ROBAK, Dr. Vestlandets forstlige Forsøksstasjon, Oslo.

ROLL-HANSEN, Jens. Statens plantepatologiske Institutt, Oslo.

STØRMER, P. Botanical Institute, Ås.